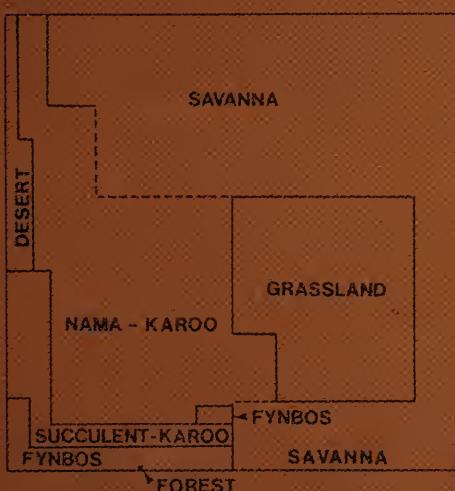


MEMOIRS OF THE BOTANICAL SURVEY OF  
SOUTH AFRICA  
MEMOIRS VAN DIE BOTANIESE OPNAME  
VAN SUID-AFRIKA

No. 54

1986

BIOMES  
OF SOUTHERN AFRICA —  
AN OBJECTIVE CATEGORIZATION



M.C. RUTHERFORD  
and  
R.H. WESTFALL

BOTANICAL RESEARCH INSTITUTE — DEPARTMENT OF AGRICULTURE AND WATER SUPPLY — REPUBLIC OF  
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by

M.C. RUTHERFORD and R.H. WESTFALL

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## **Foreword**

The classification of the vegetation of South Africa into conceptually manageable units has received the attention of a large number of botanists in the past. Whereas there is, as can be expected, a reasonable degree of convergence between these broadbased classifications, the differences in many cases were marked. The authors of the present work ascribe these differences mainly to the assumption apparently made by most authors, that subjective assessments are acceptable when working on a broad scale. The comparison of the broad scale classifications of vegetation by authors, ranging from Pole Evans (1936) to Huntley (1984) show clearly that a new approach to the delimitation of such units, on a more objective basis, was necessary. Furthermore, the use of the concept of the 'biome' by the International Biological Programme, later adopted by the National Programme for Environmental Sciences of the CSIR, as the basis of the organizational framework, made the classification of vegetation on the basis of biomes a necessity. The fact that the term biome was relatively unknown in South Africa and that no account except an unpublished note by Edwards was available, prompted Huntley to introduce the term and to briefly describe the five biomes he recognized in a short paper he published in 1984.

The authors of this memoir, Rutherford and Westfall, can be said to be the first, at least in the South African context, to have studied and defined the concept 'biome' in detail and to have delimited the South African biomes on a firm climatological basis. The thoroughness of their approach is exemplary and the result of their studies is a definitive account which should have an impact far wider than the geographical area for which it was written. It is to be anticipated that this reappraisal of the concept of 'biomes' and the new approach to their delimitation will induce ecologists to take a new look at this useful biological category.

B. DE WINTER  
Director: Botanical Research Institute

Pretoria, February 1985



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## Abstract

RUTHERFORD, M.C. and WESTFALL, R.H. 1986. The biomes of southern Africa — an objective categorization. *Memoirs of the Botanical Survey of South Africa* No. 54, pp. 98.

**Keywords:** biome, climate, life form, production, sampling method, scale, southern Africa, veld type, vegetation

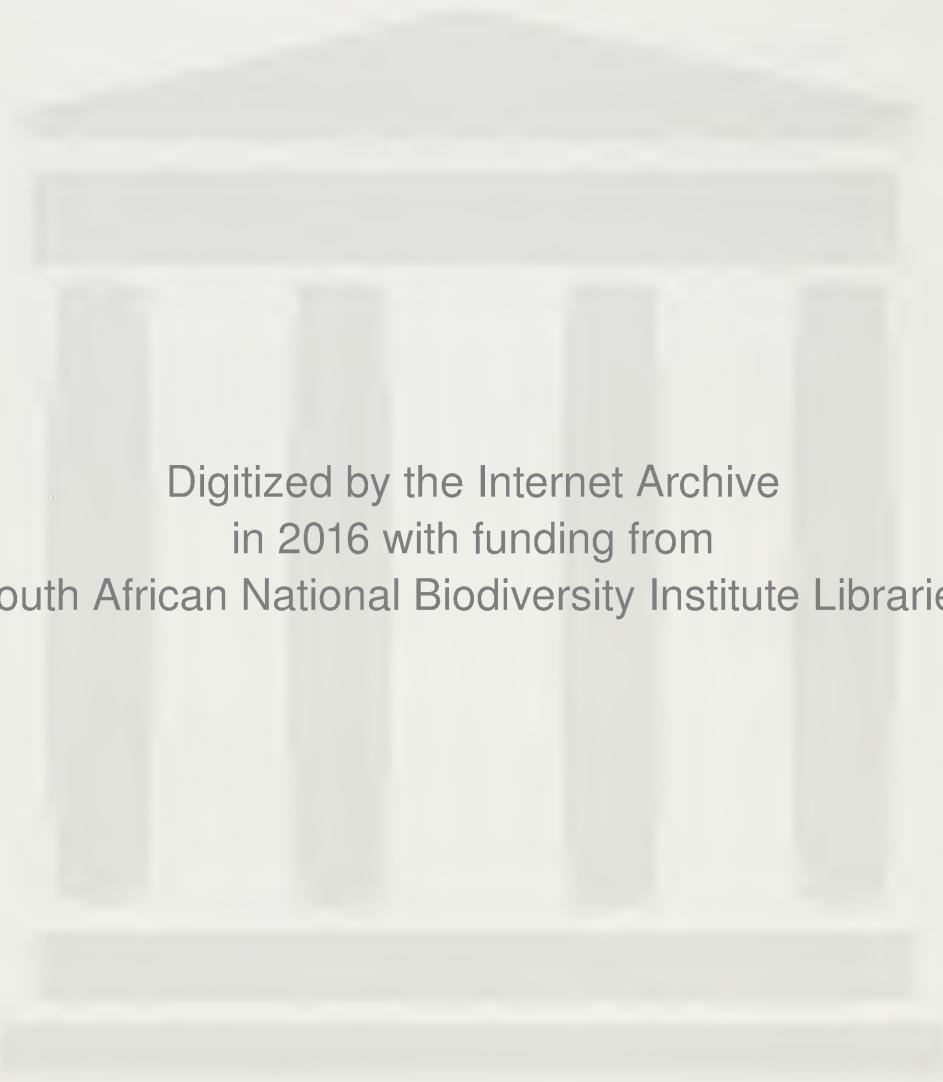
The biome concept is clarified according to established definitions to permit objective categorization of the major natural systems of southern Africa south of 22°S. Seven biomes were diagnosed according to explicit criteria of dominant and codominant plant life forms at the appropriate scale of 1:10 000 000. These are the Savanna, Nama-Karoo, Grassland, Succulent Karoo, Fynbos, Desert and Forest Biomes. The biomes correlate well with a combination of an index of summer aridity (SAI) and rainfall seasonality. This climatic combination also differentiates the biomes except for the Grassland Biome, the Forest Biome and areas of anthropogenically induced invasion of Grassland and Savanna Biomes by elements of the Nama-Karoo Biome. The Grassland Biome is differentiated climatically from Savanna in terms of minimum winter temperature in conjunction with moisture levels.

The role of zoological components in biome differentiation appears to be very limited. Absolute annual moisture levels, sometimes associated with edaphic factors, appear to form an appropriate basis for major subdivision of biomes. Ecological implications of the relationship between climate and life form dominance and codominance are discussed. Each biome is systematically described in terms of geographic, biotic, abiotic and resource relations. Various informal approaches to biome categorization in the region illustrate a general lack of appreciation of scale-dependant hierarchical levels. Problems of the relation between mapping scale, vegetation structure and floristic community are elucidated.

## Uittreksel

Die bioom-konsep word in die lig van bestaande definisies verduidelik om 'n objektiewe kategorisering van die belangrikste natuurlike sisteme van suidelike Afrika suid van 22°S daar te stel. Sewe biome is volgens bepaalde maatstawwe van dominante en kodominante plantlewensvorme gediagnoseer op die skaal van 1:10 000 000. Hierdie is die Savanne-, Nama-Karoo-, Grasveld-, Sukkulente Karoo-, Fynbos-, Woestyn-, en Woudbiome. Die biome korreleer goed met 'n kombinasie van 'n indeks van somerariditeit (SAI) en die seisoensverspreiding van die reënval. Hierdie klimaatkombinasie differensieer ook die biome, behalwe die Grasveldbiom, Woudbiom, en gebiede waar die mens indringing van Grasveld- en Savannebiome deur elemente van die Nama-Karoobiom veroorsaak het. Die Grasveldbiom is klimaties van Savanne gediferensieer in terme van minimum winter temperatuur tesame met vogtigheidsvlakte.

Die rol van soölogiese komponente in bioomdifferensiasie blyk uitsers beperk te wees. Totale jaarlikse vogtigheidsvlakte, soms met edafiese faktore geassosieer, blyk 'n geskikte basis vir die hoofonderverdeling van biome te vorm. Ekologiese implikasies van die verhouding tussen klimaat en lewensvormdominansie en kodominansie word bespreek. Elke bioom word stelselmatig in terme van geografiese, biotiese, abiotiese en hulpbronverhoudings bespreek. Verskeie informele benaderings tot bioomkategorisering in die streek illustreer 'n algemene gebrek aan waardering vir skaal-afhanklike hiérargiese vlakke. Probleme in die verhouding tussen karteringsskaal, plantegroeistruktuur en floristiese gemeenskap word toegelig.



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# 1 Perspective

## 1.1 Introduction

Many attempts have been made to reduce the great spatial and temporal complexity of man's natural environment into conceptually manageable units. Increasing subject specialization, together with global expansion, has heightened the problem of dealing with this complexity. A larger number of variables tends to obscure the significant components of large natural systems. Consensus has often been reached on the identification of narrower units of the World's natural systems, often on the basis of vegetation. At a smaller scale, however, with broader areas, consensus on units is seldom attained. Many conflicting divisions of natural systems have been proposed and mapped and most authors appear unperturbed by the plethora of differently mapped units.

Biomes are units most commonly purported in the English-speaking world to represent large, natural, reasonably homogeneous areas of the Earth's biotic and abiotic surface mantle. The importance of large units, such as biomes, is that 1, their diagnostic elements form the lowest common denominator needed for extensive comparisons; 2, they indicate the usual general limits for extrapolation of many ecological functional patterns and solutions to environmental problems within each biome; 3, they provide an initial framework for national and environmental planning and organization of scientific research; 4, they enable bias contained in certain detailed work to be viewed in a new perspective. The broad biome concept has important applications such as 1, educationally, its simplicity for the introductory phase in the complex field of environmental education; 2, sociologically, its scope and multidisciplinary nature promotes scientific intercourse for accelerated progress; 3, economically, its role in rationalizing research programmes. In special instances, resource deterioration and invasion by economically less productive components are fully recognizable at biome scale. In southern Africa, in contrast to some other regions on Earth, large areas of land are still covered by natural vegetation, so that naturally-based biomes are particularly relevant in this region.

This study attempts to categorize the biomes of southern Africa (south of 22°S) objectively. A specific effort was made to apply, consistently, each term of the original definition of a biome (see Section 1.2.1). Often these terms themselves required increased specificity. The advantages of a reasonably rigorous approach in biome delimitation appears to have been underestimated in most past work. Many researchers appear to have assumed that, at this broad scale, subjective assessments suffice. This approach suffers from lack of repeatability and allows serious bias that often reflects the regional experiences of the authors concerned. A section on methods in biome work is rarely encountered.

## 1.2 The Biome concept

### 1.2.1 Review of biome definitions

There is general agreement that a biome is a broad ecological unit (Smith 1974) that represents a major life zone extending over a large natural area (Godman & Payne 1979; Abercrombie *et al.* 1980). A biome contains a relatively uniform set of life forms (Odum 1971) or is characterized mainly by life forms (Smith 1974) with similar physiognomic types (Hanson 1962). The biotic component includes both plant and animal forms. Relevant features of the biota are closely tied to environmental conditions (Hanson 1962) and are, more specifically, determined by climate (Godman & Payne 1979) and thus reflect the major features of climate (Odum 1971).

Various other terms have been used to describe major biotic areas. According to Du Rietz (1965) the concept 'biocoenose' first used by Moebius in 1877 was employed exclusively by zoologists until it was introduced into phytosociology by Gams in 1918. Biocoenose is synonymous with 'biotic association', 'biotic community', 'biotic formation' and the 'biome of more recent North American ecologists' (Du Rietz 1965). Other related concepts are the four 'great land biochores' (Strahler 1975), the now rarely-used life zones of Merriam (Smith 1974), zoologically orientated 'biotic provinces' (Smith 1974) and the apparently multiscale 'bioclimatic units'

of Phillips (1959, 1983). Phytochoria and zoochoria (Werger 1978a) are large units based strictly on distributions of plant and animal taxa respectively. The relationship of phytochoria (a term widely used, but very differently defined) and of biomes in southern Africa is discussed in Section 6. Some biome definitions are so vague that they could be applied to almost any area. Udvardy (1975) finds this 'defendable on the basis of expediency and practicability' which is further evidence of the difficulties encountered in defining biomes on a global scale.

The definition of a biome is made explicit by referring to: 1, maximum global limits; 2, mapping scale limits; 3, the primary basis for classification; 4, the secondary basis for classification; 5, excluded areas.

A biome is:

(1) **the largest land community unit** (Odum 1971) **recognized at a continental or subcontinental level** (Hall & Day 1977). The use of superlative size makes 'biome' an absolute entity and not subject to relative repositioning in an hierarchical classification. Whereas Dansereau (1957) refers to the large unit 'biochore' (Desert, Grassland, Savanna, Forest) as being 'too large to be useful', Du Rietz (1965) counters that, contrary to those biologists, who, 'do not see the forest for all its trees', the phytosociologists of the present day agree that division of the living world into biocoenoses (= biomes) is necessary for conceiving, describing and explaining the enormous diversity and variation of the mixed organism populations. The great differences in genetic history between some continents together with limited convergence, in similar environments (see criterion No. 4) points to the advisability and sometimes necessity of limiting biome classification to continental or subcontinental dimensions. Although much classical plant geographical work tended to emphasize superficial similarities, some work on South African systems has shown, for example, that there is little convergence between 'Cape desert' and climatically analogous sites in California and Chile, or in terms of certain structural criteria. The Cape Fynbos communities show major differences from communities at climatically analogous sites on other continents (Cowling & Campbell 1980). There are also several examples of convergence in plant structure between continents in areas of widely differing climate, for example, chamaephytic (see Section 1.3) dominance in tundra and some hot deserts.

(2) **a unit mappable at a scale of no larger than about 1:10 million** (see Section 6). This means that areas or strips with shortest cross distance of less than about 20 km are too small for biome status. If an area, for example, in southern Africa, is too small to map at this scale and belongs to a recognized biome elsewhere in the continent, it has the status of a biome fragment in southern Africa. If the biome concerned occurs in southern Africa, the unmappable area has the status of a biome outlier. A biome can therefore not be restricted to a small localized area. A limit on scale for biomes is essential to comply with the requirement of large natural

areas in the original definition and eliminates local types, such as, fringing riverine forest, cliff faces and various aquatic bodies in southern Africa. The general lack of attention to scale has confused the application of many definitions of biomes. Küchler (1949) is one of the very few authors who take map scale into account when applying physiognomic classifications of vegetation. The importance of smaller scales for extensive comparisons is also illustrated by the relationship between scale and water balance of river basins where the smaller the scale the less complicated the effects of the secondary components of the water balance become (Sokolov & Chapman 1974).

(3) **distinguished from other biomes primarily on the basis of dominant life form(s) in climax systems** (Odum 1971; Smith 1974). A biome does not necessarily constitute a phytome or large plant formation and should include the animal component. The difficulty in incorporating animal 'life forms' is discussed in Section 1.2.2. It should be emphasized that as life forms form the basis for biome classification, there is no place for floristic classification here. Life forms of plants are discussed in Section 1.2.4. Seral stages of community development cannot, in terms of the definition, be considered as different biomes.

(4) **distinguished from other biomes secondarily on the basis of those major climatic features** (Odum 1971) that most affect the biota. Since there are as many climatic classifications as there are purposes, owing to the non-discrete nature of the individual climatic parameters, climatic factors are inappropriate as primary biome criteria and are used instead to correlate with distributions of life form combinations. For example, the application of simple combinations of precipitation and temperature data to form 'Holdridge life zones' results in 57 such zones in southern Africa (Schulze & McGee 1978). Many of these zones are difficult to interpret in terms of holistic natural systems. Non-climatic environmental criteria, notably edaphic ones, (which may effect (soil) climate), are usually excessively spatially variable on a biome scale. Soils can sometimes change dramatically within an area otherwise environmentally relatively uniform. The differences between plant cover on two adjacent kinds of soil are differences in floristic composition rather than in vegetation structure: soil differences determine the smaller divisions of vegetation (Adamson 1938). Heydorn & Tinley's (1980) use of edaphic criteria for biome classification cannot be supported, but obviously these may be very important in subdividing biomes (see Section 4).

(5) **not an unnatural or major anthropogenic system** and hence large areas of urbanization, cultivation and plantations are not taken into account in biome delimitation. However, systems in which man's activities (through, for example, long term severe overgrazing) have resulted in irreversible changes, are regarded as natural provided they are still self-sustaining in their present state. Application of fire by man is so common

that its net effects are regarded as natural. Dams with large water storage areas do not qualify as an aquatic biome since they are not stable and have the potential to disappear in times of extreme drought.

One area that is often treated anomalously in biome classification schemes, is that of desert. There may be some justification for defining desert less on biotic characteristics than on climate. Noy-Meir (1979/80) has hypothesized that in desert the concept of ecosystem becomes redundant and, unlike other systems, the sum of the autecologies equals the whole. Interactions between species are weak and their effects are negligible in comparison with the overwhelming effect of the weather. It is consequently not surprising that several definitions of desert use climatic parameters as primary criteria. For example, Daget (1977) suggests that true desert is characterized by an interval of more than one year between two showers of rain, a definition which applies in the Namib desert (Nieman *et al.* 1978; Pitman 1980). Zohary (1973) distinguishes between 'rain deserts' where vegetation is supported exclusively by local precipitation, and 'run-in deserts' where vegetation is supported by run-off water from nearby areas in addition to local precipitation. Walter (1979) indicates that in a desert with rainfall of 25 mm, the 'run-in' areas can receive the equivalent of 500 mm rainfall, and consequently can no longer be considered as desert. It will be seen (in Section 3.1) that application of the accepted biome definition given above results in a satisfactory delimitation of desert without recourse to climatic parameters as primary factors.

A very different departure in the use of the term biome is that put forward by Walter & Box (1976) and Walter (1979). A hierarchical system of ecological units is presented where biome is used at various levels together with a prefix. Hence we have, for example, zonobiomes (climate zones), subzono-biomes, orobiomes (mountains), pedobiomes (systems primarily dependent on the soil), lithobiomes, halobiomes and peinobiomes. The lowest levels of the hierarchy are denoted simply as biomes. Although this scheme attempts to cover global variation, it appears to suffer in having overlap of categories within the same level in the hierarchy, for example, orobiomes and zonobiomes. It is contended that it would be very difficult to objectively delimit 'biomes of higher rank' using this system at its current stage of development.

### 1.2.2 *The zoological component*

Most definitions of biomes state that dominant life forms should be the primary criterion and that animal components should be included. This leads to a schizoid anomaly. Although there is a widely recognized classification of plants into life forms since 1903 (Raunkiaer 1934), there appears to be no comparable scheme for life forms of the animal kingdom. Only Gams (1918) appears to have attempted to draw up a life form system encompassing plant and animal kingdoms (Szukla-Lacza

& Fekete 1969). His three main groups are the adnate type (ephaptomenon), radicant type (rhizomenon) and errant type (planomenon). Animals are concentrated in the last class and are subdivided on the basis of type of movement and respiratory adaptation, but this part of the scheme remains vague.

Even if one resorts to using taxonomic units of animals, what is dominance in a system with, for example, both large mammals and insects? Are data other than numbers of species available? The mobility of animals is an intrinsic problem in biome delimitation (Walter & Box 1976), and some classifications of biotic zones deliberately avoid animal densities since these can be so variable (I.L. Rautenbach pers. comm.). Most zoological-geographical treatises deal with presence and absence of animals at the species level and not with distribution of dominant elements of functional groups of animals. This often results in conflicting distribution patterns in southern Africa. For example, there is considerable disagreement between the 'Biogeographical zones' based on Coleoptera (Endrödy-Younga 1978), the 'Biotic divisions' based on amphibia (Poynton, J.C. 1964) and 'Zoogeographical subdivisions' based on avifauna (Winterbottom 1978). Werger (1978a) gives further examples of relatively divergent views on 'Zoochoria' for southern Africa. Theoretically it is expected that there should be correspondence between plant and animal since the vegetation determines, *inter alia*, the structural nature of the habitat for animals (Odum 1971). The correspondence, however, appears to depend strongly on the animal group. Rautenbach (1978a) found some correspondence for mammals whereas Liversidge (1962) found that bird distribution does not fit satisfactorily into biotic provinces and that there is little correlation between bird distributions at the species level and vegetation types. There is relatively little correspondence between broad vegetation types and many insect groups (which in animal individual numbers make up the vast majority of all animals) and distribution of these groups may be mainly determined by historical factors (C.H. Scholtz pers. comm.).

Various factors affect animal groups very differently. For example, the frost factor is important to some animal groups, but is irrelevant for the dormant stages of insects (C.H. Scholtz pers. comm.). The apparent indifference of amphibians to important ecological factors makes understanding of their distributions particularly difficult (Poynton, J.C. 1964). Poynton (1964) states that a more general picture of the biotic divisions of southern Africa is at present not possible, on account of the paucity of information about the factors determining distribution in other animal groups. Endemism of groups of animal taxa does not improve the zoological quandary where, for example, the fynbos area is distinct in terms of amphibian endemism but not in terms of avifaunal endemics (Winterbottom 1978). Smith (1974) concludes that in attempting to combine plant and animal distribution into one system, many units of classification are unworkable, because plant and animal

distributions do not coincide. Somewhat more colourfully, Darwin is quoted as follows by Haviland (Polunin 1960): 'A traveller should be a botanist, for in all views plants form the chief embellishment. But when the zoologist, forsaking botanical terms, tries to classify environments in the language of his own science, he cannot construct a workable scheme ... he finds that he must fall back on the language of the botanist or geologist'. Smith's (1974) pragmatic solution to the problem of integrating animals into a cohesive biotic scheme is to simply accept plant formations as the biotic units and to associate animals with plants, as he states, 'the distribution of animals can be related to the life form of plants and types of vegetation'. This may be a partial solution since it may account for the indirect effect of rainfall on animals through vegetation but not account for the direct effect of temperature on animals (see Poynton, J.C. 1960).

In formulating the criteria to determine the biome status of areas in southern Africa, it appears that the animal component as a whole is not necessarily a reliable criterion and that the primary criterion remains dominant plant life form(s).

### 1.2.3 *The climatic component*

The climate at any place on earth is mainly controlled by latitude, position relative to distribution of land and sea, height above sea level, general circulation of the atmosphere and its local effects, influence of ocean currents, and position relative to hills or mountains (Andersson 1969). In southern Africa, each of these factors varies greatly, except possibly for latitude which varies between 22° and about 35°S. There is less than a 10° difference for more than 90% of the land area and variation in radiation additions to the upper atmosphere is therefore limited. Climate comprises many different environmental parameters, many of which are interdependent. It is important, for the present study, to determine the effective environment of plants on an extensive basis. Any analysis to be used on an extensive spatial basis is necessarily affected by the trade-off between more precise parameters and availability of data of these parameters on a detailed network scale.

Although many climatic parameters control vegetation locally, there is much support for Walter's (1979) general statement that the most important habitat and environmental factors involved in bioclassification of the geo-biosphere are heat and water relations. In his systematic world-wide analysis of vegetation and environment, Box (1981a) found that plant form and vegetative structure are determined primarily by temperature and climatic water balance. At a continental level (Australia), Fitzpatrick & Nix (1970) found, in applying their climatic plant growth index, that only water regime had a dominant influence at almost all locations. Temperature was less important and light was rarely limiting at any station in Australia. These findings are hardly surprising when one recalls the critically important role

of water in the plant in its metabolic reactions, as a solvent, as a transporter and as a coolant. Heat affects metabolic rates, water loss and uptake rates, and can be particularly important at extreme levels. Air temperature is usually taken to indicate environmental heat levels. Plant environmental water is usually best expressed as soil moisture which is the net result of the effectiveness of precipitation. This again is affected by many factors, one of the most important being the effect of temperature on water losses to the atmosphere. Runoff, physical soil characteristics, slope and other factors are often important locally. One of the simplest attempts at reflecting effective annual precipitation has been to account for the inverse effect of increased temperature on available water as  $P/T$ . This form has been applied as an 'aridity index'  $H$  where

$$H = P/(T + 10)$$

where  $P$  = annual precipitation in mm and  $T$  = annual mean temperature in degrees C (De Martonne quoted in Tuukkanen 1980). A less misleading aridity index ( $A$ ) uses the reciprocal of the basic form namely

$$A = 100T/P$$

(Dantin & Ravenga quoted in Tuukkanen 1980). On a monthly basis, Walter (1979) uses  $P \leq 2T$  after Gaussen to define periods of drought.  $P \leq 3T$  is used for periods of less critical dryness (Trockenzeitz). In his review of climatic indices, Tuukkanen (1980) refers to very many other, often more complex, indices including those using temperature sums, potential evapotranspiration, precipitation-temperature relations, precipitation-evaporation relations, duration of dry conditions, number of precipitation days and continentality/maritimity estimates. Further description of these indices is not repeated here.

In southern Africa, various climatic indices have been applied or derived. Phillips's (1983) much publicized bioclimatic units of southern Africa use various climatic parameters and do not include a single synthetic climatic index. Schulze & McGee (1978) have pointed out limitations of the well known system of Köppen as applied to southern Africa. The same authors's application of Holdridge's climatic life zones to southern Africa, shows some uninterpretable complex results. More complex indices are often designed for local use in cropland areas. For example, Scotney & De Jager (1971) put forward an Environmental Potential Index (EPI) based on soil moisture deficit, available heat and rainfall variability. The Palmer Drought Index is gaining popularity in South Africa (Booysen & Rowswell 1983) but, due to the limited number of suitable climatic stations, this index can not be determined for many parts of the region. The lack of suitable data is exemplified by an attempt by Louw & Kruger (1968) to apply Penman's equation, as modified by Montieth, to South Africa where the data were such that the validity of the estimates could not be proved. A basic difficulty is to

obtain suitable simultaneous data for a sufficient number of places over a long enough period. The use of 73 stations for South Africa (Preston-Whyte 1974), for example, is obviously insufficient for mapping biomes and their borders.

An increasing number of climatic indices appear to have been employed at random with little regard for existence of other indices or for practicality of application. In numerous works, it is implied that a particular climatic expression is very different from another, whereas they frequently correlate closely (Tuhkanen 1980). Reitan & Green (1968) have commented that many such indices give 'about the same answers'. It is refreshing to read Tuhkanen's (1980) comments: 'one cannot speak of indices being correct or incorrect. Unnecessary complexity is definitely to be avoided in the construction of indices of this kind. One should always aim at simplicity, all the more so when the data are such that they do not permit extended elaboration'. Yet he finds that 'a number of indices are discussed ... which would be extremely inconvenient to use due ... to the lack of the necessary data'.

The long established network for measuring precipitation in southern Africa is not particularly detailed and for some regions is altogether inadequate. The temperature-measuring stations form a small subset of this network and there are many areas, sometimes with distinctive vegetation transitions, for which no temperature data are available. Temperatures are strongly dependent on the location of the weather stations (Poynton, R.J. 1971) and large microclimatic differences, for example in winter, temperature minima can make some of the temperature stations unrepresentative for their region. In view of these disadvantages, a parameter was sought for use in the present study, in which the effect of temperature on moisture would be reflected without the explicit incorporation of temperature. The importance of water as a limiting factor during a physiologically important period is emphasized. The importance of drought or arid periods has been widely recognized and, for example, Hounam *et al.* (1975) list more than 50 different measures of drought.

Details of the application of climatic factors used in the present study are given in Sections 2.3 and 2.4. Primarily, a moisture matrix of a Summer Aridity Index (SAI) and Winter concentration of precipitation was applied, which maximized use of the available data station network. Where this matrix was found inadequate to explain certain important changes in vegetation, limiting temperature data from the smaller network of temperature stations was used in the form of mean lowest minimum temperature for the coldest month.

The Summer Aridity Index (SAI)\* is defined as the sum of the mean precipitation for the four hottest months of the year, taken as a natural logarithm for scaling purposes and subtracted from a constant to

ensure ascending values with increasing aridity. This index reflects moisture at a physiologically important time of year and under conditions of high evaporative demand. The advantage of using the four hottest months is:

(1) they are continuous, that is the four months constitute a single time period;

(2) the months are geographically consistent, that is, for broad areas of southern Africa the four hottest months can be confidently predicted at stations measuring rainfall only;

(3) the range of mean temperature of the period of the four hottest months is not excessive over the relatively restricted, defined area of southern Africa with its limited range of latitude;

(4) the period of the hottest four months was found, by trial and error, to be more satisfactory than (a) the period of the hottest three months, which is sometimes more varied spatially than the four month period and possibly less limiting and significant to some plant types, or (b) the period of the hottest five months, which is also more varied spatially and is affected by the much more variable adjacent sixth and seventh hottest months.

The index is summarized by:

$$SAI = 9 - \ln \left[ \sum_{i=1}^4 P_i \right]_{t_{\max}}$$

where  $P$  is mean monthly precipitation in mm. A logarithmic transformation is used because moisture parameters tend to be more critical in determining the main life form combinations at the lower range than at the upper range of moisture.

In areas with winter rainfall, intermediate rainfall and with mainly but not pronounced summer rainfall, application of the SAI is straightforward. In the last-mentioned area, the four hottest months coincide with the four wettest months. However, in the pronounced summer rainfall areas the amount of rainfall in the wet season is physiologically important. In these areas the four hottest months overlap to a large extent with the four wettest months and application of the SAI formula is modified slightly to account for such shifts (see Section 2.3.1).

The SAI is similar to the Summer Drought Stress (D) of Mitrakos (1980) where

$$\begin{aligned} 2(50-p) &= MDS \\ D &= \Sigma MDS \end{aligned}$$

where MDS = Monthly Drought Stress and Summer Drought Stress (D) = June (MDS) + July (MDS) + August (MDS) (in northern hemisphere) where  $p$  is monthly precipitation in mm and  $D$  is set to 0 when  $P \geq 50$ .

SAI differs in that it does not contain the arbitrary limit of 50 mm, below which information on the degree

\* SAI is an aridity index which refers to mean moisture conditions and is not a drought index which reflects irregular periods of subnormal rainfall.

of drought stress is lost, nor is it tied to fixed summer months which are not necessarily always the hottest.

SAI is basically a measure of moisture stress for a period which is potentially well suited to optimum plant physiological performance. It is felt that any less crude an index would cease to make full use of the available station network without which climatic correlation, especially in certain areas of biome transition, would not be possible.

The second axis of the moisture matrix involves seasonality of rainfall in the form of winter concentration of precipitation (R) (Bailey 1979) where

$$R = \frac{\text{sum of winter half precipitation}}{\text{(mean annual precipitation)}}$$

with six winter months (April to September). Although May to October is sometimes used as winter half year (Aschmann 1973), the period April to September is that used historically in South Africa, for example, by Adamson (1938), the South African Weather Bureau (for example Schulze, B.R. 1965) and on other continents (for example Russell & Moore 1976). The R-factor is fully applicable to southern Africa since all five of Bailey's (1979) classes of R are present, namely, strong winter ( $\geq 81\%$ ), winter (61–80%), even (41–60%), summer (21–40%) and strong summer ( $\leq 20\%$ ). The importance of winter rainfall in the climatic classification of South Africa is indicated by the work of Preston-Whyte (1974) who used an array of 24 climatic variables and found that the most important of the four resulting complex indices was that for winter rainfall which explained the highest percent of the total variance. The degree of concentration of winter rainfall tends to correlate with elements of continentality and the shift from cyclonic to anticyclonic climatic patterns and their associated attributes. Seasonality of rainfall has also been shown to be directly significant for certain biological groups. For example, in the Karoo areas, it has been found that grass forms are overwhelmingly responsive to summer rain, *sensu stricto*, whereas growth of dwarf shrubs is mainly determined by rainfall outside the main summer period (Vorster & Roux 1983). Grasses prefer high minimum air temperatures for active vegetative and reproductive growth in the Karoo (Vorster undated). Many other plant adaptations to rainfall seasonality are relatively unresearched. For example, in winter rainfall areas there are adaptations to localized water-logging, lower physiological rates under cooler conditions and a preponderance of C<sub>3</sub> over C<sub>4</sub> photosynthetic pathways in certain plant groups.

The winter concentration of precipitation is a proportion and is not seen as a particularly sensitive index on its own, but, combined in a matrix with the SAI, it assumes much greater significance for correlation with vegetation elements.

It is strange how seasonality of rainfall receives no explicit attention in most climatic indices. Even in those indices which allow for seasonality of rainfall, the

treatment is often scant and arbitrary. For example, in Köppen's extensively used index for defining 'dry climate', seasonality is accounted for by merely taking P < 2t for regions of winter rain, and P < 2t + 14 for regions of summer rain where p = annual precipitation in cm and t = mean temperature in °C (Hounam *et al.* 1975).

The mean daily temperature was not used since this parameter is relatively insensitive for vegetation correlation. Temperature extremes are far more important (than mean daily temperatures) as limiting factors. In southern Africa, temperature minima are usually more limiting than maxima. Mean highest maximum temperatures for the hottest months are mainly between 30° and 40°C and rarely exceed 40°C, and the mean lowest minima for the coldest months are mainly between -5° and +5°C. Many plants are tolerant of this range of maximum temperatures but are adversely affected by the lower part of the range of minima with the change in state of water. For this reason, the minimum temperature was the parameter selected for vegetation correlation but cognizance was taken of different moisture levels that may influence the response of vegetation to temperature minima.

The temperature minimum used was the mean lowest minimum temperature for the coldest month, which appears most appropriately to express the limiting effect. This parameter has also been successfully used by Henning & White (1974) for correlation with certain plant distributions. This form is closely related to daily minimum temperatures (Hinds & Rotenberry 1979) (see Section 2.4). Absolute lowest minimum recorded temperature was not used because of its susceptibility to freak events and consequently greater variability.

#### 1.2.4 *The plant component — review of life forms*

Nearly all life form systems tacitly assume the following broad principles (Cain *et al.* 1959): (1) plants have different ecological amplitudes or tolerances; (2) the physiological integration of the total environment is needed for a plant's successful existence; and (3) there is often a correlation between morphology and adaptation. 'Life form' is determined by general physiognomy whereas 'growth form' is a subdivision based on the architecture of the shoot (Du Rietz quoted Adamson 1939). Life forms are reportedly equivalent to the 'ecobiomorphs' used by certain Soviet workers (Fekete & Szukla-Laczka 1970). It should be noted that there is no generally accepted classification of plants into growth forms, which is presumably one of the reasons for emphasizing life forms in biome definitions. One of the most recent and different growth form classifications is that of Box (1981a). He distinguishes 19 main structural types which he subdivides into 77 'life forms'. It is a rather cumbersome system when compared with that of Raunkiaer (discussed below), and does not recognize geophytes or therophytes as classes exclusive of other forms.

Of all the life form schemes put forward, that of Raunkiaer has received most attention and has been applied to a wide variety of vegetation types (Adamson 1939; Cain 1950) and is still in general use today (Fekete & Szukla-Lacza 1971). This scheme has the combined advantages of simplicity, consistency and ease of application (Adamson 1939). Raunkiaer's main principles concerning the characteristics of life forms are (Fekete & Szukla-Lacza 1971); the character must represent something fundamental in the plant's relationship to climate; it must be fairly easy to use and easily categorized in nature; and it must represent a single aspect of the plant to facilitate a comparative treatment of the vegetation of different regions. Only those structural characters that reflect the essential dependence of the plants upon climate are used (Szukla-Lacza & Fekete 1969). Raunkiaer's emphasis on the climatic association was so strong that he intended to characterize different climates on the basis of life forms (Fekete & Szukla-Lacza 1971). Main climatic emphasis was on adaptation to survive the unfavourable season in accordance with the Law of Minima (Szukla-Lacza & Fekete 1969). Braun-Blanquet (quoted Du Rietz 1931) indicated that in some circumstances, plant adaptation to climate may depend less on the unfavourable season than on the favourable season, presumably where the unfavourable season is not severely limiting. Although Raunkiaer recognized the need for finding the ideal plant life form which is the sum of its adaptations to environment, he pragmatically proposed that only one essential adaptation be used for characterizing life forms (Fekete & Szukla-Lacza 1971). The importance of the abundance of individuals of a life form rather than species, for correlating with the climate of a given area, was not initially recognized (Raunkiaer 1934). The relative proportion of life forms should be expressed in terms of plant abundance ('physiognomically, by the form which dominates by its mass', Raunkiaer 1934) and not in terms of species number ('biological spectrum') for this purpose.

Raunkiaer saw the quantitative adaptation to the unfavourable season as manifesting itself principally in the reversible reduction of plant organs (Fekete & Szukla-Lacza 1971) in which the defence and protection of shoots and buds in the unfavourable season is important (Szukla-Lacza & Fekete 1969). Although seldom explicitly stated in Raunkiaer's original scheme, the unfavourable season was that mainly of low heat levels and temperature minima in the temperate zone. His five main life form classes were associated with areas of major changes in these climatic parameters, namely, with microclimatic zones near the ground. His classes are based on the height of the perennating buds of the plant relative to the ground surface. The classes are (Cain 1950):

*phanerophytes*, which have their bud-bearing shoots elevated and exposed to the atmosphere and are with few exceptions woody trees and shrubs;

*chamaephytes*, which have their perennating buds closer to the soil surface but definitely above the soil surface;

*hemicryptophytes*, which have their buds at the surface of the ground;

*cryptophytes*, which have their buds beneath the soil surface and include the important geophyte group; and

*therophytes*, which are annual plants that survive the unfavourable season in the form of seed.

Zohary (1962) has questioned the validity of Raunkiaer's five basic life forms in arid regions and states that emphasis should be put not on the protection of the buds but on the protection of the whole plant body against drought. He quotes Orshan who in 1953 provided four alternative life forms for arid areas based on the reduction the plant body undergoes during the unfavourable season. One of the life forms of Orshan has been subdivided, which results in five life forms. These life forms have been applied to parts of the winter rainfall area of South Africa (Orshan *et al.* undated). Although the principles and rationale are different in deriving Raunkiaer's life forms and Orshan's life forms, it is clear from Orshan (1983) that, in practice, the five classes of the two systems are virtually identical. The following correspondences are indicated; phanerophytes and leaf shatters; chamaephytes and acropetal branch shatters; hemicryptophytes and basipetal branch shatters; cryptophytes and shoot shatters; and therophytes and plant shatters. Leistner (1967) applied Orshan's divisions in the southern Kalahari and remarks that we 'still arrive at groups which agree largely with life forms of Raunkiaer'. Cain (1950) simply accepts that in Raunkiaer's life form system, unfavourable seasons may be due to cold or drought or both. Sarmiento & Monasterio (1983) question the applicability of Raunkiaer's system to savanna, but their proposed three main 'morphofunctional groups' are essentially simplifications of Raunkiaer's five main classes. The ground surface as reference plane for major life form categories is theoretically sound in that climatic gradients are usually steepest near the ground. Substantially different climatic conditions exist less than 2 m above ground, for example: the speed of wind is reduced by friction with the ground and hence there is less mixing of the air; the ground surface absorbs radiation and is a source of heat itself; and ground surface is a source of water vapour (Geiger 1965). That the majority of life form classes are close to the ground surface and that only a single broad phanerophyte class is further from the ground surface (Fig. 1) is in keeping with these gradients. The upper limit of Raunkiaer's chamaephyte class is only 0,25 m above ground. Many workers have found that this limit, within the climatic gradient near the ground surface, is too low and have in practical application used a higher height limit. A height of 0,8 m is suggested as the highest limit for location of renewal buds (Orshan 1982) and for total height including annual branches (Du Rietz 1931). The height limit may be extended to 1,0 m 'for classificatory reasons' (Mueller-Dombois & Ellenberg 1974) as applied in certain areas of southern Africa by Orshan *et al.* (undated).

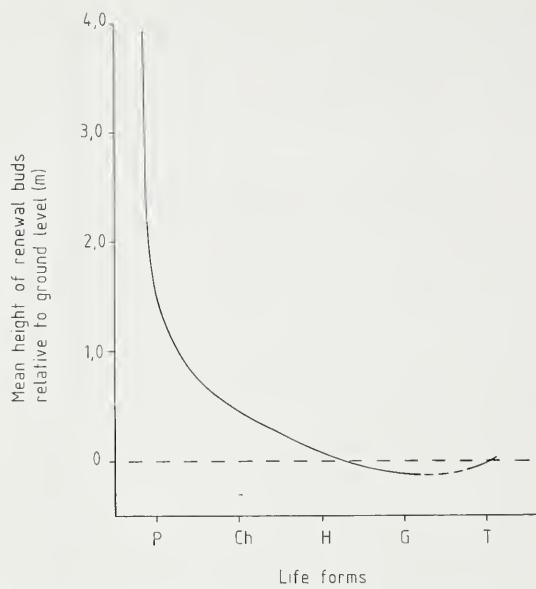


FIG. 1.—The relationship between life form and mean height of renewal buds relative to ground level (after Schmidt, 1969). Abbreviations for life forms are: P, phanerophyte; Ch, chamaephyte; H, hemicryptophyte; G, geophyte; and T, therophyte. The horizontal dashed line represents ground level. The discontinuity in the relationship between geophyte and therophyte is indicated by the curved, broken line.

There is general agreement that the primary division of phanerophytes should be based on plant height but some differences exist in the choice of height limits. For example, the height classes of the phanerophytic divisions of Raunkiaer (1934) have been changed by Mueller-Dombois & Ellenberg (1974) as follows:

Phanerophytic subdivision	Raunkiaer	Mueller-Dombois & Ellenberg
Megaphanerophyte	>30 m	>50 m
Mesophanerophyte	8–30 m	5–50 m
Microphanerophyte	2–8 m	2–5 m
Manophanerophyte	<2 m	<2 m

For specific local use, various other height classes are used. In savanna, for example, the units of Edwards (1983) are shrubs (phanerophytes <2 m), trees (phanerophytes >5 m) and an overlapping class of shrubs and trees. The last-mentioned class is, therefore, 2–5 m based on structure (Edwards 1983) or 2–5.5 m based on production relations (Rutherford 1982).

Szukla-Lacza & Fekete (1972) conclude that Raunkiaer's life form concept is the theoretically best substantiated and the system most consistent in design.

The argument that the system of Raunkiaer 'suffers from rather difficult Greek terminology' (Polunin 1960), cannot be regarded as really valid. A more valid terminological criticism is that of Orshan (1982) who showed that the perennating bud is not necessarily identical to

the renewal bud. This applies especially in some chamaephytes of hot arid areas in which most of the renewal buds do not pass the unfavourable season as buds. Orshan therefore suggests that the term renewal bud should be used. Because of the usual difference between height of the renewal buds and that of the top of the plant canopy, various apparently equivalent terms for plant life forms are not necessarily equivalent. The term dwarf shrub, for example, cannot necessarily be used synonymously with the term chamaephyte.

Where the occurrence of fire is seen as the unfavourable season, plants may be classified into fire life forms (Van der Merwe 1966) which depend upon the height of the renewal buds following the fire. Plants can be classified very differently by life form and fire life form. For example, a phanerophyte life form such as *Protea repens*, is classified as a therophyte fire life form since it survives fire in the form of seed. The possible relationships between life forms and fire life forms are shown in Fig. 2. Therophytes can correspond only to fire therophytes (where fire occurs) and geophytes correspond almost exclusively to fire geophytes which reflects the highly effective adaptation of geophyte individuals to fire.

The use, in plant taxonomy, of consistent and conservative plant characters which are relatively independent of climate has led to a widely accepted

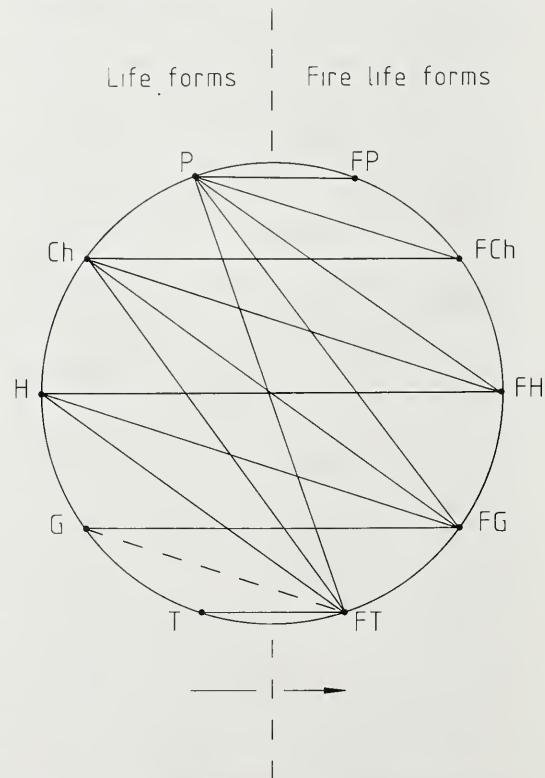


FIG. 2.—The relationship between life form and subsequent fire life forms. Abbreviations used are: P, phanerophyte; Ch, chamaephyte; H, hemicryptophyte; G, geophyte; and T, therophyte. Fire life forms are preceded by an F.

classificatory system. This has sometimes tended to obscure the main object of the plant ecologist's endeavour which is to establish plant-environmental relationships. Pre-Linnaean taxonomy had a large element of life form description for its basis. With the development of the Linnaean sexual system of classification, vegetative structures were relegated to a very minor role, but in modern times, form has regained some of its former importance (Cain 1950). Andreánszky comments strongly on taxonomists being biased in preferring the value of the generative organs at any price, and in neglecting the taxonomic importance of habit (Szukla-Lacza & Fekete 1972). Dansereau (1957) even suggests that Raunkiaer's 'essential merit was in breaking away from taxonomic units'. On the other hand Böcher (1977) states that the structures of the reproductive parts show similar biological groupings, 'clearly equivalent to life forms'. However, his concept of 'life-form' is not comparable and includes forms such as 'fruit life-form' and 'flower life-form'.

Raunkiaer (1934) subdivided his five main life form classes into 30 subtypes. However, he reduced this number of subtypes to 10 classes to establish relations with climate. These classes are:

1. Mega- and Mesophanerophytes
2. Microphanerophytes
3. Nanophanerophytes
4. Epiphytes
5. Stem succulents
6. Chamaephytes
7. Hemicryptophytes
8. Geophytes
9. Hydrophytes and Halophytes
10. Therophytes

In view of the above discussion on climatic gradients being much less pronounced above 2 m than closer to the ground, phanerophytes should rather be retained as a single major class, as has been done with chamaephytes and hemicryptophytes. Because epiphytes are host-dependent, the height of their renewal buds depends on the height of the host which is contrary to the tenets of the system. The exclusion of leaf succulents from the stem succulent class has drawn comment. Various workers, for example, those quoted by Adamson (1939), Van der Merwe (1966) and Leistner (1967), have found it necessary to extend the class to include all succulents. Succulents have long been regarded as a distinct group, both on structural and physiological grounds (Adamson 1939). Daubenmire (1974) classifies plants into three main classes based on water relations, that is, hydrophytes, xerophytes and mesophytes. The importance of succulents is recognized in the widely recognized xerophyte class which is divided into ephemeral annuals, succulents and non-succulent perennials. However, as with epiphytes, the height of renewal buds in succulents can vary from ground level to many metres and despite its possible functional significance, it is difficult to

support this class as equivalent to, for example, chamaephytes or hemicryptophytes. In southern Africa, at biome scale, the class of hydrophytes and halophytes (a subclass of cryptophytes) is inadequately represented. For these reasons, not all the 10 reduced subtype classes of Raunkiaer have adequate standing as major classes and the original five life form classes remain valid.

Raunkiaer limits the application of his system to vascular plants (Adamson 1939). An attempt to include some non-vascular groups in an expanded version of this system (Mueller-Dombois & Ellenberg 1974) has yet to gain general acceptance. In most terrestrial systems, non-vascular plants are relatively insignificant.

Raunkiaer's system deals with the plant shoot alone (Adamson 1939). It has been felt, that to obtain any real expression of the reactions to environment, the underground portion must be included (Adamson 1939). Consequently, root life form systems have been proposed (Du Rietz 1931; Kazakevich, quoted Fekete & Szukla-Lacza 1970). Apart from the impracticability of dealing with root systems on an extensive basis, there are doubts as to the life form value of the generally more facultative and locally opportunistic below-ground plant component, in comparison with the more deterministic and predictable relationships of the above-ground plant component with climate.

Raunkiaer's relationship between life forms and climate tacitly assumes that life forms evolved in the present prevailing climate. The distribution of the climate could have been different at the time when the life form of a species developed. The effect of past climates can result in anomalous relationships between the life form present and the current climate of an area, although the speed of adjustment (evolutionary or migratory or both) to climatic change can be such as to negate the effect of this factor in many instances. In the shorter term, lack of correspondence between plant life forms and climate can often be attributed to the historical vegetation utilization practices of man.

Although the geophyte class is a logical component of Raunkiaer's system, Raunkiaer found that no main plant climate exists that is characterized by cryptophytes (geophytes). The cryptophytes are to be considered complementary to a hemicryptophyte climate (Fekete & Szukla-Lacza 1971). By contrast, the chamaephyte class is one that has been regarded as of definite importance as a climatic indicator (Adamson 1939). Hagerup (quoted Adamson 1939) has, for example, claimed a high chamaephytic percentage as an indication of semi-desert as distinct from desert conditions.

### 1.3 Definitions of life forms used in this study

A synopsis of definitions of life forms and their abbreviations used in the present study is given below for ready reference. Many published definitions that use height of the renewal (or perennating) buds do not state whether maximum or mean height of buds on a plant is intended. Furthermore, in plant populations,

mean height of all above-ground renewal buds is not necessarily equal to the mean height of the top-most buds. In the present study, mean height of all above-ground renewal buds of the plant populations is accepted as the standard.

**Phanerophytes** (P): Perennial plants, usually woody, with the mean height of the renewal buds greater than 0,7 m above ground level. Because plant height is usually greater than the mean height of renewal buds, the mean plant height of phanerophytes is seldom less than 1,0 m.

**Chamaephytes** (Ch): Perennial plants, generally woody or partly woody, with the mean height of the renewal buds less than or equal to 0,7 m. Following the rationale applied in phanerophytes, mean plant height of chamaephytes is seldom greater than 1,0 m.

**Hemicryptophytes** (H): Perennial plants, generally herbaceous, with the renewal buds at or, more often, close to ground level, but seldom exceeding 0,1 m in height.

**Cryptophytes** (G): Perennial plants, usually herbaceous geophytes, with renewal buds below ground level. Since, in this study, only geophytic cryptophytes are considered, the term geophyte is used henceforth.

**Therophytes** (T): Ephemeral plants that complete their entire life cycle in one year or less.

#### 1.4 Characteristics of life forms

The relationship between life form and mean height of renewal buds relative to ground level has been given in Fig. 1. The range of typical morphological types within each life form is indicated below together with a short list of example taxa for southern Africa. These taxa illustrate the practical classification of life forms. It should be noted that some of the taxa are often borderline cases and are placed in the class into which they most frequently fall.

Phanerophytes include a wide range of morphological types, for example, single-stemmed trees, larger multi-stemmed shrubs, palms, tree ferns, bottle trees, bamboos, lianas and plants resembling the banana plant. However, only the first two forms are significant in southern Africa at biome level. These forms can be subdivided into evergreen and deciduous groups and fine-leaved and broad-leaved groups.

Example taxa of phanerophytes include: *Acacia tortilis* (Forssk.) Hayne, *Adansonia digitata* L., *Burkea africana* Hook., *Combretum molle* R. Br. ex G. Don, *Commiphora africana* (A. Rich.) Engl., *Cunonia capensis* L., *Cyathea dregei* Kunze, *Dalbergia armata* E. Mey., *Dichrostachys cinerea* (L.) Wight & Arn., *Euphorbia ingens* E. Mey. ex Boiss., *Grewia flavescens* Juss., *Hypaene natalensis* Kunze, *Ilex mitis* (L.) Radlk., *Podocarpus falcatus* (Thunb.) R. Br. ex Mirb., *Portulacaria afra* Jacq., *Protea repens* (L.) L., *Rhus lancea* L. f., *Sclerocarya birrea* (A. Rich.) Hochst. subsp. *caffra* (Sond.) Kokwaro, *Strelitzia nicolai* Regel & Koern., *Strophanthus speciosus* (Ward & Harv.) Reber, *Tarchonanthus*

*camphoratus* L. and *Thamnochalamus tessellata* (Nees) Soderstrom & Ellis.

Chamaephytes include dwarf shrubs, low succulents and cushion plants. Typical taxa are: *Barleria bremekampii* Oberm., *Chrysocoma tenuifolia* Berg., *Cyphostemma bainesii* (Hook. f.) Desc., *Erica dominans* Killick, *Erica nudiflora* L., *Eriocephalus ericoides* (L. f.) Druce, *Euphorbia mauritanica* L., *Haworthia attenuata* Haw., *Helichrysum trilineatum* DC., *Hereroa hesperantha* (Dinter) Dinter & Schwart., *Metalsia muricata* (L.) D. Don, *Pentzia incana* (Thunb.) Kuntze, *Plinthus karooicus* Verdoorn, *Rhigozum trichotomum* Burch., *Stoebe vulgaris* Levyns and *Sutherlandia frutescens* R. Br.

Hemicryptophytes include perennial graminoids, aphyllous restioids and perennial broad-leaved herbs (forbs). Typical taxa are: *Cenchrus ciliaris* L., *Dicliptera clinopodia* Nees, *Ficinia nigrescens* (Schrad.) J. Raynal, *Gazania krebsiana* Less., *Gerbera jamesonii* H. Bol. ex Hook. f., *Heteropogon contortus* (L.) Roem. & Schult., *Staberoha cernua* (L. f.) Dur. & Schinz, *Thamnochortus dichotomus* (Rottb.) R. Br. and *Themeda triandra* Forssk.

Geophytes include plants with bulbs, corms, tubers, non-graminoid rhizomes and root-stocks as well as geoxyllic suffrutices. Typical taxa are: *Crinum bulbispermum* (Burm. f.) Milne-Redh. & Schweick., *Dichapetalum cymosum* (Hook.) Engl., *Dipcadi gracillimum* Bak., *Fadogia monticola* Robyns, *Herschelia spathulata* (L. f.) Rolfe, *Kniphofia linearifolia* Bak., *Oxalis flava* L., *Wachendorfia paniculata* Burm. and *Watsonia densiflora* Bak.

Therophytes include herbaceous graminoids and forbs that are annual or ephemeral. Typical taxa are: *Cenia turbinata* (L.) Pers., *Chironia purpurascens* (E. Mey.) Benth. & Hook. f., *Cleome monophylla* L., *Eragrostis viscosa* (Retz.) Trin., *Helophilus coronopifolia* L., *Perotis patens* Gand., *Rhynchelytrum repens* (Willd.) C.E. Hubb., *Sebaea grandis* (E. Mey.) Steud., *Setaria pallide-fusca* (Schumach.) Stapf & C.E. Hubb., *Stipagrostis subacaulis* (Nees) De Winter, *Tribulis terrestris* L. and *Wahlenbergia capensis* (L.) A. DC.

Life forms form a natural sequence from phanerophytes through chamaephytes and hemicryptophytes, to therophytes in respect of several characteristics (Fig. 3). Such sequences are, however, subject to great variation, especially if no distinction is made between life forms from different biomes. Geophytes are omitted from this sequence because of insufficient data relative to some of the characteristics. Mean plant age (age of the whole plant) usually decreases from phanerophytes through to therophytes (Fig. 3a). By comparison, mean youth period (the period from germination to formation of first seed) also tends to decrease from phanerophytes to therophytes but to decrease more strongly from phanerophytes to chamaephytes than from hemicryptophytes to therophytes (Fig. 3b). Hemicryptophytes, therefore, may reach early reproductive capacity despite their relative longevity. The mean age of the above-ground material in hemicryptophytes (Fig. 3c) is, however,

much lower than the age of the whole plant, which may indicate a closer relationship between youth period and above-ground age than between youth period and whole plant age. The youth period relationship confirms that phanerophytes require considerably longer periods to reproductive maturity and are more vulnerable to longer term unfavourable episodic events for establishment. The proportion of annual production allocated for generative reproductive purposes is generally lowest for phanerophytes with an increasing proportion to therophytes but with the largest increase from hemicryptophytes to therophytes (Fig. 3d). Up to 50% and an even greater proportion of (annual) production allocated to generative reproduction, has been reported for therophytes (Schulze, E.D. 1982). This emphasizes the dependence of therophytes on surviving unfavourable periods in the form of seed. In contrast, phanerophytic populations can afford to endure a number of years without re-establishment from seed. The ratio of annual production to biomass (above-ground) increases fairly evenly from phanerophytes through to therophytes (Fig. 3e) and indicates the decreasing importance of accumulated structural material from phanerophytes through to therophytes. Accumulated structural material, in turn, sets the potential limits for the bearing height of the renewal buds of each life form respectively. Accumu-

lated structural material can be proportional to storage material which then supports the findings of decreased resilience or increased susceptibility to unfavourable conditions in the growing season from phanerophytes through to therophytes (Fig. 3f). Henrici (1931) found, in the Karroid area, that adverse conditions, like drought or frost, affect the grasses to a much greater extent than the bushes.

The ratio of below-ground mass to above-ground mass (root/shoot ratio) (Fig. 3g) differs from the other direct or inverse relationships mentioned above. The root/shoot ratio, generally increases from phanerophytes through to hemicryptophytes but then often decreases in therophytes. There is therefore an inverse relationship between height of renewal buds and root/shoot ratio for perennial plants (and this relationship would be strengthened with inclusion of geophytes). Obligate annuals and ephemerals invest little growth below ground which results in a lower root/shoot ratio than that in hemicryptophytes. But in facultative annuals, that is, annuals which can become perennials with a fairly limited life span, the root/shoot ratio can be similar to that of hemicryptophytes. The former annual group is an example of r-selection (Grime 1979) where growth is rapid and of short duration and the proportion of energy devoted to reproduction is large. The latter

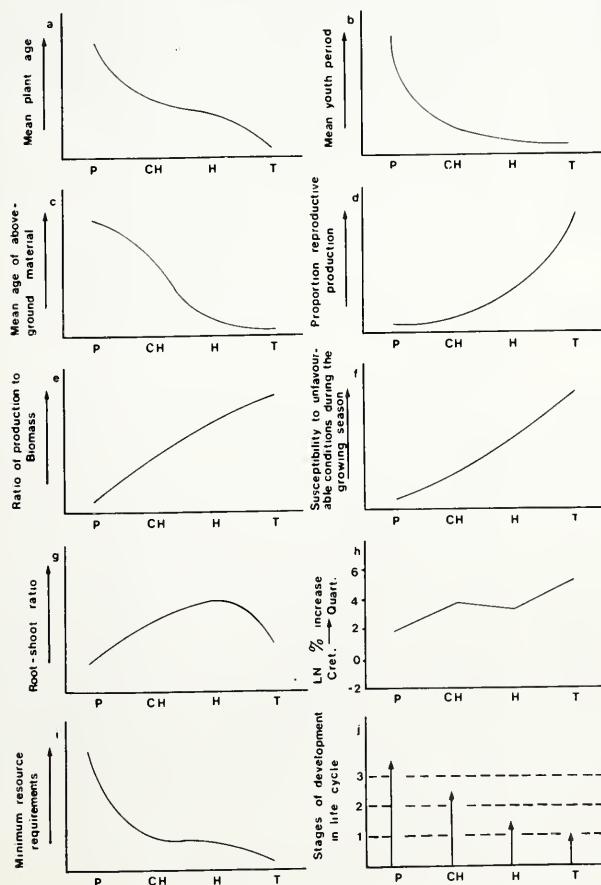


FIG. 3.—Generalized relationships between life form sequence according to height of the renewal buds and plant ecological properties: a, mean plant age; b, mean plant youth period; c, mean age of above-ground material; d, the reproductive proportion of production; e, ratio of production to biomass; f, susceptibility to unfavourable conditions during the growing season; g, root-shoot ratio; h, natural logarithm of the percentage increase of plant genera from the Cretaceous to the Quaternary periods; i, minimum plant individual resource requirements; and j, stages of development in the life cycles of the life forms. Abbreviations for life forms are: P, phanerophyte; Ch, chamaephyte; H, hemicryptophyte; G, geophyte; and T, therophyte.

group tends toward the perennial plants's K-selection where growth is slow and of longer duration and the proportion of energy devoted to reproduction is smaller.

There appears to have been a more recent proliferation of the smaller life forms since the Cretaceous period (Fig. 3h) (Hanson, quoted Szukla-Lacza & Fekete 1972). This indicates increased specialization and adaptation to new conditions in the direction of smaller perennial plants and therophytes as well as indicating that r-selection is evolutionarily recent. Adamson (1939), quoting Bewes, recognized that the more advanced types of life form are those associated with more arid habitats.

Minimum resource requirements are usually markedly greater in phanerophytes than in chamaephytes and hemicryptophytes and least in therophytes (Fig. 3i). Minimum resource requirements of individual plants include those of water and space. Thus, for example, mean plant stem spacing within populations of the same life form tends to decrease from phanerophytes through to therophytes.

Stages of development in the life cycle of each life form are indicated in Fig. 3j. Whereas phanerophytes normally proceed through all stages, the remaining life forms are limited to differing extents. Therophytes, by definition, cannot proceed to the hemicryptophytic stage. Hemicryptophytes normally proceed beyond the therophytic stage but if minimum resource requirements are not met, they can be restricted to the latter stage. Chamaephytes and phanerophytes can proceed to further stages and similarly can be restricted to earlier stages of development under certain conditions. These considerations are sometimes very important in determining life forms in different areas (Raunkiaer 1934).

The above selection of characteristics of life forms indicates that the life forms used, are fundamentally, functionally different and that each plays a significant, ecological role.

## 1.5 Previously proposed biomes for South or southern Africa

Biomes or natural biotic divisions of first level have been proposed by many authors for South and southern Africa. A selection of 21 of these, that represents various approaches since 1936, have been included for analysis and are specified in Table 1. Prior to 1936, most major subdivisions of southern Africa were based on very incomplete data (see examples from 1823 in Werger 1978a). Units in Table 1 are limited to first levels of division and were matched *sensu lato*, that is, if the main concept or main area of the units coincided (usually at least 75% overlap of surface area). Where necessary, anomalies are indicated in Table 1. No account was taken of terminology used but text descriptions of units were consulted to evaluate some smaller units, especially forest, and in two cases where units were not mapped.

Data were arranged chronologically and according to frequency of use of the unit in four groups, namely: I, those five units with frequency of more than 40%

which, incidentally, together account for the entire area; II, two combinations of some units in I; III, 15 smaller units, often subdivisions of units in I; and IV, 26 unique units, proposed only once in the data set (Table 1). It is clear that some authors have relied upon the units of others but have often altered the rank of the divisions, for example, some of Schmithüsen's (1976) mapped units bear remarkable resemblance to several parts of Keay (1959). Tinley (1975) recognizes a division into only two superunits or 'major life divisions' namely, 'Afrotropical' and 'Tropical' but, appropriately, his six biomes are used in the same sense as in the present work. Similarly Huntley's (1984) seven mapped biomes are taken instead of the five biomes that could be derived from the text. The mean number of units proposed for southern Africa is 7.1. One third of the classifications reflected contains at least one unique type that does not occur elsewhere in the data set.

Despite difficulties in reconciling apparently highly diverse divisions, considerable pattern of these divisions nevertheless emerges. The only units that are used, without aforementioned anomalies, by more than half the sources, are Fynbos and Grassland. With the inclusion of some anomalies, only two more are used by more than half the sources, that is, the Arid Zone and Forest, and Savanna is used by almost half the sources. These five most frequently used units are depicted in relation to some less frequently used units in Fig. 4. Desert is clearly the next most frequent unit. The inclusion of purely South African classifications with southern African data sets probably results in underrepresenting the border units of 'Desert' and 'Tropical Lowland Forest'.

Those subdivisions of the five most frequently used units that have been elevated to major unit status by at least two of the sources are summarized in Fig. 5. Those who agree on recognizing the Kalahari area as a major unit, usually have a variety of other major savanna units, most of which are unique to each source. The only proposed division of savanna that does not result in a plethora of unique units, is the division into Arid and Moist Savannas.

Five authors, namely, R.S. Adamson (1938), J.F.V. Phillips (1959), H.P. van der Schijff (1971), D. Edwards (published by Van der Meulen & Scheepers 1978)\* and Tainton (1981), limit their classification to the five most frequently used units. It is remarkable that only these five authors agree on number and identity (not terms) of the major divisions, whereas there is no total agreement between any of the other 16 proposed schemes. The work of these authors illustrates a recurring popular biotic theme which has run as a thread through time. Huntley's (1984) major divisions, which have the same rank as some of his lower divisions, correspond to these five most frequently used mapped units but the status of these units is not indicated on the map. Rautenbach's (1978a) units are also similar to these major units but are not mapped.

\* Drawn by Edwards in 1970, presented at Rinteln in 1972 and published in 1981 (Edwards & Werger 1981).

TABLE 1.—Major natural biotic divisions proposed by 21 representative sources for South and southern Africa. Data are arranged chronologically and according to frequency of occurrence of the divisions within the whole data set in four groups: I frequency of more than 40%; II combinations of divisions in I; III smaller divisions, often subsets of divisions in I; IV unique divisions proposed once in the data set

Source	Date	Area	Scale of map <sup>1</sup> (X10 <sup>-6</sup> )	Major natural biotic division according to source	No. of divisions (+ - not mapped)	% unique divisions proposed within the whole data set	Units, with convenient descriptors e.g. Fynbos, Grassland etc., based on approximate area correspondence of natural biotic divisions and on parsimony (see also Fig. 4)															Source							
							Group I					Group II					Group III					Group IV							
							1 Fynbos	2 Grassland	3 Arid zone	4 Forest	5 Savanna	6 Grassland and savanna	7 Fynbos and forest	8 Desert	9 Afro-alpine	10 Afromontane forest	11 Kalahari	12 Karoo (excluding desert)	13 Succulent Karoo	14 Main Karoo	15 Subtropical lowland forest	16 Subtropical and tropical lowland forest	17 Tropical lowland forest	18 Aquatic	19 Arid savanna	20 Eastern seaboard savanna	21 Mangrove	22 Moist savanna	23 Unique natural biotic divisions
Pole Evans	1936	southern Africa	1:3	Vegetation	4	0																							
Adamson	1938	South Africa	1:8	Vegetation	5	0	Bush (Sclerophyll)	Grassland	Desert Shrub	Semi-Desert	Forest	Parkland <sup>2</sup>																	Pole Evans
Moreau	1952	Africa	1:63	Biotic type = Biotic division = Biome	3+1	0																							Adamson
Acocks <sup>4</sup> (Veld type map)	1953	South Africa	1:1,5	Veld type group <sup>5</sup>	7	43	Sclerophyllous Bush Types	Grassveld Types	Karoo and Karroid Types <sup>6</sup>			Tropical Bush and Savanna Types (Bushveld <sup>2</sup> )																	Moreau
Acocks <sup>4</sup> (Acocks map No. 2)	1953	South Africa	1:7	Vegetation	10	40	Macchia	Temperate and Subtropical Grassland			Forest and Scrubforest																		Coastal Tropical Forest Types; Inland Tropical Forest Types; Acocks <sup>4</sup> (Veld type map)
Keay	1959	Africa south of the Tropic of Cancer	1:10	First Division vegetation	13	38	Cape Macchia																						Mixed Grassveld; Scrubby mixed Grassveld; Sour Grassveld; Sweet Grassveld
Phillips <sup>4</sup>	1959	Africa south of Sahara	1:20	First Division Bioclimatic Region	5	0	Macchia (Fynbos)	Open Grassland and Grassland	Subdesert and Desert	Forest	Wooded Savanna																	Keay	
Eyre	1963	southern Africa	1:21	Major Vegetation type	8	13	Cape sclerophyllous scrub	Open Grassland and Veld																				Phillips <sup>4</sup>	
Meester	1965	southern Africa	1:20	Main biotic zone	4	0	South-West Cape					Evergreen mixed forest <sup>7</sup>																Eyre	
Van der Schijff	1971	South Africa	1:20	Biome	5	0	Fynbos or Macchia	Grassveld																				Meester	
Tinley	1975	Africa	1:57	Biome	6	0																						Van der Schijff	
Schmithüsen	1976	Africa	1:25	Vegetation	17	41	Sclerophyllous shrub formation	Subtropical upland grass steppe																			Tinley		
Rautenbach	1978a	southern Africa		Biotic zone	0+6	0	South West Cape	Southern Savanna Grassland	Dwarf & Succulent Shrub	Forest and Forest	Southern Savanna Woodland																Rautenbach		
Van der Meulen & Scheepers <sup>4</sup>	1978	South Africa	1:13	Vegetation	5	0	Shrub	Grassland	Karoo-Namib Region	Scrub-Forest	Deciduous Tree or Thorn Savanna & Thicket																Van der Meulen & Scheepers <sup>4</sup>		
Wenger	1978a	southern Africa	1:30	First Division Phytochorion	6	0	Capensis																					Wenger	
Tainton	1981	South Africa	1:8	Formation	5	0	Macchia (Fynbos)	Grassland																			Tainton		
White <sup>4</sup>	1981	southern Africa	1:5	Phytochorion	7	43	Cape regional centre of endemism		Karoo	Forest	Savanna																White <sup>4</sup>		
Pienaar	1982	southern Africa	1:10	Biome	5	0	Sclerophyll formation or Fynbos																				Pienaar		
Scheepers <sup>4</sup>	1982	South Africa	1:14	Biome	12	25	Fynbos	Grassland																					
Huntley	1984	South Africa	1:14	Biome	7	0	Fynbos	Grassland	Karoo																		Scheepers <sup>4</sup>		
Backer et al.	In press	southern Africa		Biome	0+8	0	Fynbos	Grassland		Forest	Woodland/Savanna/Scrub																Huntley		
x			1:18,4																									Backer et al.	
n			19																										
n			7,1																										
n			21																										
Total number of divisions					18		14		13		12		10		4		2		8		4		4		3		2		
% of total number of sources					86		67		62		57		48		19		10		38		19		19		14		10		
Number of anomalies included in total (see footnotes)					0		0		3		2		2		1		1		2		0		0		0		0		

<sup>1</sup> Some of the larger scales are suited to more detailed subdivisions than to first level divisions

<sup>2</sup> These divisions do not extend southwards to the eastern Cape but only extend to northern Natal

<sup>3</sup> Very broad, extending much further north

<sup>4</sup> Acocks (1953) republished Acocks (1975) and (1988); Phillips, J. 1959 republished Phillips, J.F.V. (1983); Van der Meulen & Scheepers (1978) republished Edwards & Wenger (1981); White (1981), text published White (1983); Scheepers (1982) republished Scheepers (1983), and with modified terminology. Report of the Planning Committee of the President's Council on Nature Conservation in South Africa (1984)

<sup>5</sup> Including False Types  
<sup>6</sup> Extends as patches up eastern seaboard valleys to central Natal

<sup>7</sup> Southern Cape only with no other forest categories  
<sup>8</sup> Afromontane only with no other forest categories

<sup>9</sup> Includes other montane vegetation  
<sup>10</sup> Includes grassy Karoo

<sup>11</sup> Overlaps with others of its own units

<sup>12</sup> North of 22°S, this is mainly an inland type

<sup>13</sup> Extends much further south

<sup>14</sup> Unusually restricted

<sup>15</sup> Assumes no change north of South Africa in Mozambique

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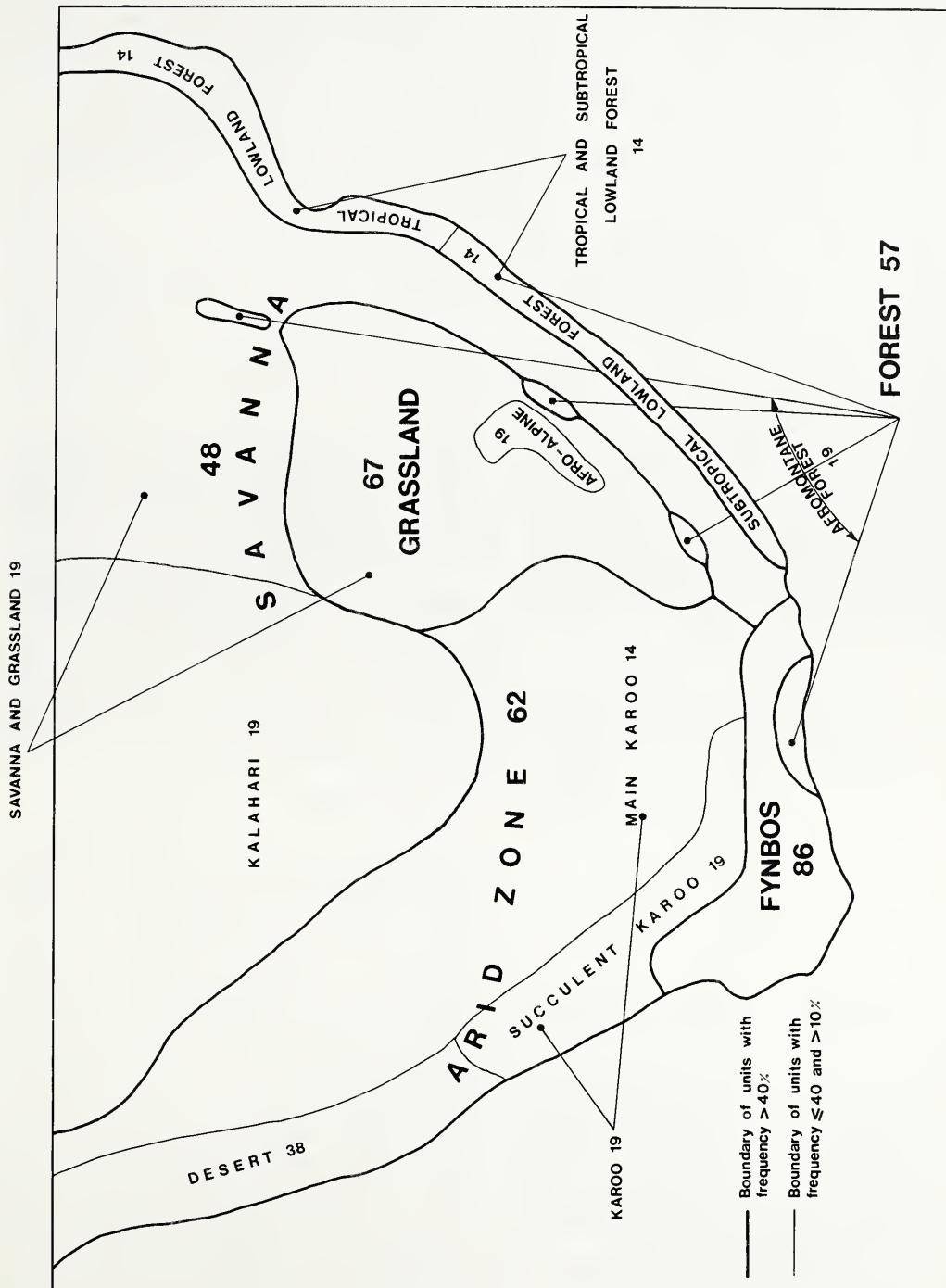


FIG. 4.—A schematic representation of the frequency (%) of first level divisions of vegetation/ecosystems in southern Africa as proposed by 21 representative sources since 1936. Units with a frequency of only 10% or less are omitted (see also Table 1).

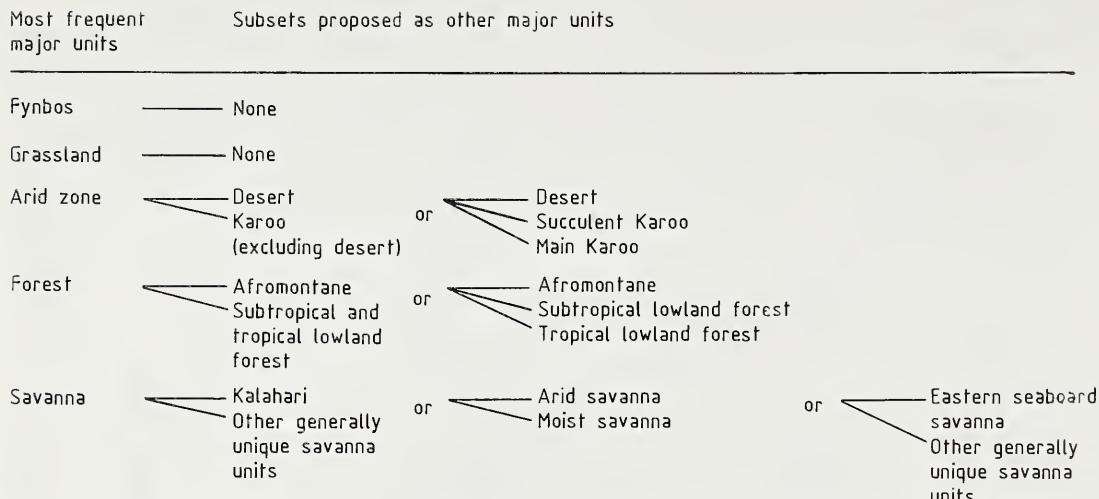


FIG. 5.—Most frequent first level divisions of southern Africa (major units) and subsets proposed since 1936 as major units by more than one source (see also Table 1).

When other authors are also taken into account, trends are apparent in the use of these five units (Fig. 6). Use of Fynbos and Grassland has increased steadily, whereas only that of the Arid Zone has steadily decreased. The latter indicates an increasing realization that aridity can result in very diverse biotic adaptations and lead to subdivisions of the arid zone. Recognition of Forest and Savanna units has been more variable.

published earlier. Terms for the Arid Zone and Savanna are the most variable. Use of the term biome has increased in recent years. In the last 15 years, half of the sources refer to major first divisions as 'biomes' in contrast to about 10% previously.

It is important to note that the schematic map given in Fig. 4 is based purely on popularity and that in the works used most authors give no indication of the criteria employed in their classification. It is one of the main aims of the present work to ascertain to what extent there is correspondence between popular subjective divisions and units obtained through objective application of defined criteria.

#### 1.6 Concluding remarks

The biome concept has been clarified according to established definitions and it is clear that there are many first level divisions that do not qualify as biomes. This is usually for reasons of inadequate size, inappropriate scale, insufficient attention to life form dominance, undue attention to supposed climax conditions and lack of explicit correlation with climatic features. The limited role of the zoological component in the concept of biomes has been substantiated. For successful biome classifications, methods based solely on zoological parameters should be avoided and much more emphasis should be placed on the vegetation component. The importance of climatic in contrast to non-climatic (e.g. edaphic) criteria for confirmatory correlation at biome scale has been highlighted because of the dependence of life form on climate. The most important climatic components identified were water and heat. Despite the large number of indices of water and heat, many of these are redundant, impossible to apply or irrelevant to major biotic response. Climatic indices appropriate to a specific objective should be employed or developed. The fundamental and most widely accepted life form system of

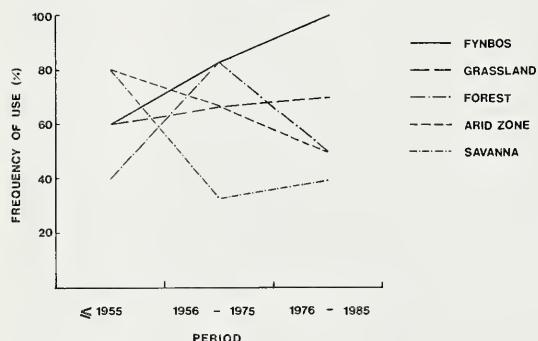


FIG. 6.—Trends in the frequency of use of the five first level divisions of southern Africa with the greatest mean frequency.

Fynbos is the most widely recognized distinct first level division. This suggests that it is an accepted norm for the range of variation that a single major unit can contain. This is surprising, since the Fynbos area has great diversity in plant structure and floristic concentrations, a mean annual rainfall that can vary by a full order of magnitude, and other important features (see Section 4.4).

There is a remarkable lack of standardization of terminology of units and sometimes identical terms are used for different areas. The most consistently used terms for the most frequently used units, are Forest, closely followed by Grassland (or Grassveld). The term Fynbos has tended to replace the Sclerophyll or Macchia

Raunkiaer (1934) formed the cornerstone for biome differentiation. A certain amount of concept development was found necessary for practical implementation and led to an expanded ecological basis for these forms. The various past classifications of first-level divisions of southern Africa based on subjective assessments show remarkably great disparity in terms of concept, terminology and delimitation of the divisions.

In the search for alternative or confirmatory functionally significant plant life form classifications, it is striking how few ecophysiological works address this subject. The ecophysiological literature abounds with various isolated aspects of the plant. The work often deals with no more than the physiology of parts of the plant which happen to be in the field and there is limited temporal integration and often no spatial integration. Only in very few ecophysiological works are results correlated with relative degree of success of plants in their habitat. There are cavalier references to representativeness of data which imply applicability to very broad areas. Very rarely have the problems of determining the limits of extrapolation of an ecophysiological model been indicated for changes of soil type, vegetation treatment and history, slope, etc. Modern ecophysiology at biome scale is almost non-existent and even whole plant studies under field conditions are relatively rare.

Orians & Solbrig (1977) suggest that physiological

data on costs and incomes associated with (life) forms of plants are seldom available because most physiologists concentrate on ways organisms adapt to environment. The assessment of costs of these mechanisms is more difficult and of less physiological interest. Lange *et al.* (1981) refer to a philosophical wedge being driven between physiology and ecology in the earlier part of the present century. The potential of ecophysiology was very much suppressed until fairly recently with the development of new measuring devices suitable for the field. Ecological physiology, according to Lange *et al.* (1981) is, consequently, 'no longer a somewhat suspect and scarcely accepted offshoot of physiology or ecology'. However, the full potential of ecophysiology has yet to be realized. The modern complacency found in much of current ecophysiology is, fortunately, becoming increasingly punctuated with admissions of the need to put the ecology into ecophysiology. Lange *et al.* (1981) express the fascinating hope that ecological physiology may facilitate meaningful integration of autecology and synecology. Larcher (1980) suggests various levels of integration while cautioning that in future, plant ecophysiology will be important in controlling the limits of ecological generalizations and extrapolations. Ecophysiology, the field of study that should form a fundamental functional basis for delimitation and analysis of biomes, has yet to contribute significantly to advancement in this field.



## 2 Methods

### 2.1 Determination of dominant life forms

The presence or absence of the dominant life forms was determined from numerous sites or broader areas south of 22°S from published and unpublished surveys, inventories, maps, annotated photographs and reconnaissances of 91% of the number of veld types in South Africa and all of the South West African/Namibian vegetation types, together with interviews, consultation and correspondence with various researchers (see also Acknowledgements) in various sectors of southern Africa. The area of study was limited to those latitudes for which data were more readily available and which included the whole of the Republic of South Africa and permitted a subcontinental analysis.

Life forms of plants alien to southern Africa were excluded. Emphasis was placed on existing vegetation and not on supposed climax vegetation which formed an important part of Acocks's (1975) concept of veld types. No attempt was made to reconstruct vegetation composition from the distant past or to speculate on climaxes in the absence of evidence. 'The interpretation of vegetation in terms of climax considerations is often extremely difficult or impossible' (UNESCO 1973).

Data on geophytes are very scanty and incomplete in most vegetation surveys. The practical identification of life forms was sometimes difficult. Height of renewal buds was not necessarily constant and could vary according to annual environmental changes. Similar to Adamson (1939), it was found that some species had more than one life form according to plant age or habitat. Some species populations were predominantly transitional between two life forms, such as chamaephytic/phanerophytic *Elytropappus rhinocerotis* (L. f.) Less. These problems were only relevant when these populations were dominant or codominant. It is also important to emphasize that it was often not necessary to assess dominant life forms of areas on a species basis. Where the relative contribution of life forms changed considerably with succession, only vegetation at stages that tended to persist longest over broad areas, was considered. This was particularly relevant in Fynbos where life form composition is age dependent (Moll *et al.* 1980).

Vegetation is primarily determined by dominant

species (Du Rietz 1931). The commonly used life form spectra do not necessarily reflect life form dominance (Adamson 1939; Cain 1950). Dominance or codominance of a life form was determined at biome scale on the basis of the relative contribution to total mean annual production, but weighted according to a hierarchy where phanerophytes and chamaephytes have a greater influence in the community than hemicryptophytes and geophytes which, in turn, are greater than therophytes (analogous to Box's (1981a) growth form dominance hierarchy). This scheme partly compensates for the effect of considerably lower Biomass Accumulation Ratios (Whittaker 1970) in hemicryptophytes and geophytes than in phanerophytes and chamaephytes (see also Section 1.4). Unidominance was determined accordingly for the following groups where minimum relative contributions to total production are weighted; P > 75%; Ch > 75%; H > 90%; G > 90%; T > 95%. If none of these levels were attained, codominance occurred when the sum of the relative contributions of the two life forms with the highest contribution was greater than the lower of the two life forms weighted production values. If this sum was not greater than the lower value, then the life form with the next highest contribution was added and tested against the lowest of the three life forms weighted production values. In this way, either one, two or three life forms were designated as dominant or codominant. The probability of one non-dominant life form constituting the entire balance of production, is low, where the balance is usually spread over several life forms. Where one non-dominant life form makes up the major portion of the balance of production, a biome interface is usually indicated.

Shimwell (1971) states that dominance and codominance is expressed in terms of biomass or, in general ecology, in terms of foliage cover. Although either of these two parameters is often useful in expressing dominance, their application can result in under- or over-estimating the relative importance of certain life forms in some areas. For example, in forest vegetation, use of foliage cover can overestimate the importance of a ground layer relative to the dominant upper strata; in areas where the codominant grass group is heavily grazed, use of biomass or cover can underestimate its re-

lative importance, and in areas where therophytes are common, use of foliage cover can overestimate their relative importance. Use of plant productivity is closer to Shimwell's (1971) concept of physiological dominance.

Determination of plant productivity at a large number of individual sites is often difficult and impracticable, so that few such data are available. However, estimates of productivity for small scale application need only be approximate. This is because reduced detail allows greater emphasis on use of mean values than on that of local extremes. Productivity (or its estimating parameters) of plant groups is less variable at a small scale than at a large scale. Moreover, at small scale, relative values of productivity of vegetation components are less variable than absolute values. Various aids were available for estimating plant productivity at small scale — these included: productivity—plant structure relations, particularly using the more widely available foliage cover data; productivity models; productivity partitioning ratios; and productivity—biomass proportions. Resultant productivity estimates are therefore often merely functions of appropriate parameters with more readily available data. Where life form composition was such that it was obviously not critical for diagnostic purposes, it was not necessary to even convert data to productivity estimates.

## 2.2 Determination of biomes

The total number of all life form combinations ( $N$ ) is given by

$$N = \sum_{i=1}^n \left[ \begin{matrix} n \\ i \end{matrix} \right]$$

which for five life forms gives 31 combinations or potential biomes. These combinations were screened for occurrence at biome scale. Geophytes were found neither as dominants nor codominants at this scale, thus leaving four life forms for consideration. Therophytes were found to be dominant but not codominant in combination with other life forms at this scale. Areas where therophytes and other life forms were codominant were only narrow unmappable strips or belts on the biome scale. It follows that the potential number of biome units in southern Africa is much reduced. The remaining number of combinations is given by

$$N = \sum_{i=1}^3 \left[ \begin{matrix} 3 \\ i \end{matrix} \right] + 1$$

which in turn gives eight potential biomes in southern Africa. This reduced number of possibilities assisted in utilizing less detailed information sources to categorize life form combinations for areas with no better data.

As defined, minimum area for life form dominance was that with a shortest cross distance of 20 km. In

biomes with more than one dominant life form, these were required to be codominant in any given area of at least this size. In a mosaic of areas with different dominant life forms, the area was classified after that part of the mosaic with the larger area and single conglomerative biomes were not created. If any member of a mosaic exceeded an area with a shortest cross distance of 20 km, it was obviously mapped separately. Patterns of the distribution of life forms or groups of life forms were partly correlated with the veld types of Acocks (1975) and vegetation types of Giess (1971) which were used to help map boundaries (in South Africa and South West Africa/Namibia), although modifications were often required.

In areas with very low rainfall and little vegetation, the relative proportions of life forms can be more variable because of the very low productivity values concerned. In the present study, data from these areas were limited to rain desert areas (Zohary 1973). Run-in areas, including drainage lines and depressions, were excluded.

In applying the 20 km shortest cross distance requirement for biomes, a problem arose where the shortest cross distance for the largest fragment of the fragmented forest biome was slightly less than 20 km (Fig. 7). For purposes of biome recognition and representation, the main fragment was consolidated and mapped. An aquatic biome was not recognized since the shortest cross distance of the largest water body was considerably less than 20 km.

## 2.3 Determination of climatic patterns

Climatic data have recently become available on a computer data base of the Weather Bureau, Pretoria, South Africa. Only this data base was used for determining climatic patterns in the Republic of South Africa and the TBVC areas. Data for other southern African countries as well as for selected world stations, were obtained from Meteorological Office (1958a,b, 1959, 1966, 1967, 1972). Data from the world stations were used to indicate some similarities and dissimilarities with the southern African data set. Seasonality of rainfall becomes irrelevant near the equator and in extreme deserts ( $SAI > 8.5$ ). All southern African data were evaluated for consistency and, consequently, several stations were rejected. Means calculated for the maximum number of available years for each station were used. The minimum number of years accepted is specified below.

### 2.3.1 Rainfall

Precipitation data from 1755 stations were used (Appendix 1). Each station had at least 20 years of data except for a few areas where no such station existed. In these cases stations with just under 20 years' data were accepted. For each station the following was obtained or calculated:

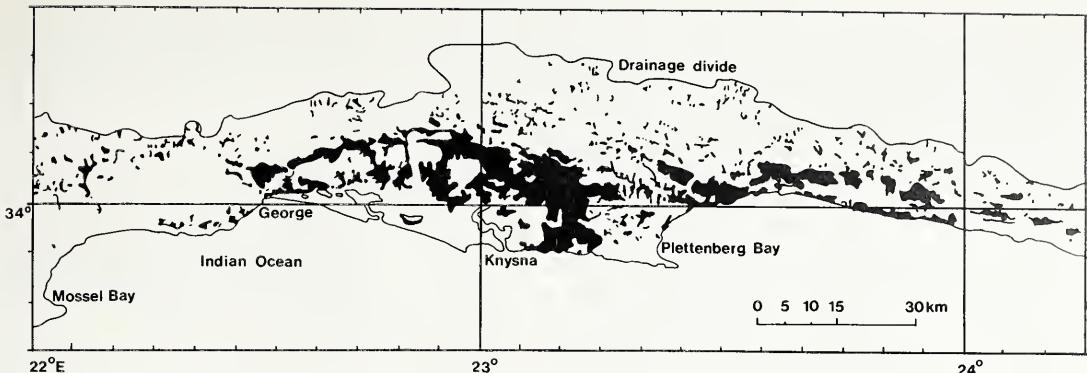


FIG. 7.—Distribution of indigenous forest patches in the southern Cape which includes the largest forest patch in southern Africa south of 22°S (Scriba 1984).

- (1) Mean annual rainfall
- (2) Seasonality: the percentage of mean annual rainfall in the winter half year (April to September inclusive)
- (3) Mean summer half year rainfall (October to March inclusive)

(4) Summer Aridity Index (SAI). This index was designed for application where summer drought is more important and where the hottest four months period were markedly hotter than that of adjacent months, and reflected a period of maximum potential water stress to plants. The application was modified by using the four wettest months in the moister inland areas of southern Africa (central SWA/Namibia, far northern Cape Province and Botswana, central and northern OFS, Transvaal, Zimbabwe, north-western Natal and inland Mozambique). Here maximum rainfall quantities are more important than the four hottest months which may not contain the rainfall maxima. However, in most of the transitional areas between the two applications, the four hottest months were identical to the four wettest months, therefore ensuring an essentially smooth transition of SAI across the subcontinent.

### 2.3.2 Temperature

Temperature data from 105 weather stations (Appendix 2) were used. Each station had at least 11 years of data except in a few areas where no such stations occurred and slightly less than 11 years's data were accepted. Temperatures are strongly influenced by location of weather stations (Poynton 1971). In areas with several stations in relatively close proximity and where discrepancies in minimum temperature between some of these stations existed, those stations which reflected the mean values for that area were accepted. These discrepancies are largely due to variations in local topography. For example, in the Johannesburg municipal area, temperature minima between stations varied by more than 10°C as a consequence of local topography (Goldreich 1971).

For each station, the following were obtained or calculated:

- (1) Identity of the four hottest months in terms of mean daily temperature for each month, calculated as  $(TX + TN)/2$  where TX is daily maximum temperature and TN is daily minimum temperature.
- (2) Mean lowest minimum temperature for coldest month.
- (3) Mean daily minimum temperature for coldest month (for comparison with the last mentioned parameter).

### 2.4 Integration of biome units and climatic pattern

A moisture matrix of SAI (which indirectly includes a temperature component — see Section 1.2.3) and winter concentration of precipitation (seasonality) was used for graphical correlation with life form combinations expressed as vegetation or veld types which were sometimes modified (see Fig. 10). This form of representation is termed a 'climagram' by Nahal (1981). Each data element represents a rainfall station for which the vegetation is known. Although the data from 1755 stations (Appendix 1) were utilized, only a representative selection of these is given in the graphical synopsis. The selected stations outside southern Africa are included in this synopsis but were not taken into account in establishing the relationships between climate and biomes. Biomes were delimited purely on the basis of life form combinations. Where fewer data points were available, the delimiting line was less definitive. The upper limit of SAI for occurrence of forest patches is shown. The maximum summer aridity limits of dominance or codominance of each life form are indicated. Mean annual rainfall isolines that correspond to certain limits of vegetation are included. These lines were obtained through correlation (omitting non-southern African stations) with parameters of the graph axes and are, therefore, approximate. Where biomes were not distinguishable in terms of the moisture matrix, a second matrix which incorporated direct temperature data, was used.

The axes of the second matrix are mean summer half year rainfall amount (October to March) and mean lowest minimum temperature for the coldest month.

The amount of rainfall, and not a proportion, was used following the direct inclusion of temperature and its role in affecting available moisture. The amount of rainfall in the summer half year was selected since the biomes that were not distinguished in terms of the moisture matrix, occurred in summer rainfall areas. Lines delimiting biomes were drawn but because of the fewer number of stations available, these lines are generally less definitive than in the moisture matrix. The mean lowest minimum temperature for the coldest month (LMN) was tested for similarity against, for example, daily minimum temperature for the coldest month (TN). The high positive correlation ( $r = 0,98$ ) between these two parameters indicated that it was not critical which of the two parameters was used. The relationship was  $TN = 5,0824 + 0,8588 LMN$  (in  $^{\circ}C$ ).

Various climatic interpretations were also aided by

Detrended Correspondence Analysis (DCA) (Hill & Gauch 1980) ordinations of the life forms and biomes.

## 2.5 Concluding remarks

The methods described are not qualitative but quantitative and therefore have enhanced predictive value. Because the vegetation-climate relationship is so complex, it cannot be expressed in simple algebraic terms, but the matrices used in this study can be digitized and the biomes determined algorithmically.

Although the present study's climatic data input was basically limited to the Weather Bureau data base of early 1984, future analyses can make use of an expanded data base of the Division of Agrometeorology, Department of Agriculture and Water Supply, which incorporates the former data base.

### 3 Analysis of results

#### 3.1 Life forms and biomes

The combinations of dominant life forms found in southern Africa at biome scale are shown by means of a set diagram (Fig. 8) where each of the four basic sets represents a life form. Life form codominance is shown by intersection sets. Unidominance of phanerophytes, chamaephytes, hemicryptophytes or therophytes represent the Forest, Succulent Karoo, Grassland or Desert Biomes, respectively. The intersections of phanerophytes and hemicryptophytes; chamaephytes and hemicryptophytes; and phanerophytes, chamaephytes and hemicryptophytes represent the Savanna, Nama-Karoo and Fynbos Biomes respectively. The intersection of phanerophytes and chamaephytes was found to be a null set. A total of seven biomes was thus obtained. Limited intersections of hemicryptophytes and therophytes and of chamaephytes and therophytes were found but were not mappable at biome scale. The DCA ordination of life forms (Fig. 9) confirms on the first axis the separation of therophytes from the other life forms and this corresponds to the sole dominance of therophytes without any codominance (Fig. 8).

Cain *et al.* (1959) provide a scheme in which life forms and their combinations are compared with world vegetation units. It is particularly interesting to compare the results from the present study with this independent scheme because of similarities in approach. As in the present study, Cain *et al.* (1959) found no dominance or codominance of geophytes in world systems and this life form was excluded from their scheme. Similarly they also did not find a combination of phanerophytes and chamaephytes. Six of the seven biomes categorized in the present study were identifiable in the scheme of Cain *et al.* (1959). The seventh biome, namely Fynbos, has three codominant life forms for which no provision was made in the scheme of Cain *et al.* (1959). The three main components of developed Fynbos were already recognized by Adamson (1938) and are widely accepted as a recurring feature in Fynbos (for example Boucher 1978). The combination of hemicryptophytes and therophytes of Cain *et al.* (1959) is of limited extent in southern Africa (see above) and they do not indicate a combination of chamaephytes and therophytes. The

remaining combination of phanerophytes and therophytes of Cain *et al.* (1959) is probably an anthropogenically induced unit, but may occur as small, isolated patches along a desert margin and is definitely not of biome proportion.

Some examples of life form composition in specific sites are given for each biome in Table 2 where it was unnecessary to convert the cover data. It is clear that in such life form abundance spectra, abundance is concentrated in fewer life forms than in floristic 'biological' spectra where species are more evenly distributed across life forms (for example Adamson, 1939).

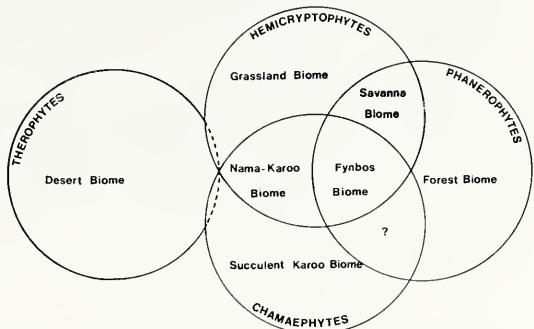


FIG. 8.—Set diagram of four main life forms, illustrating how the sets and their intersections differentiate biomes.

#### 3.2 Climate and biomes

The three most arid biomes in terms of the moisture matrix (Fig. 10), namely, Desert, Succulent Karoo and Nama-Karoo, are individually distinct from each other. The Fynbos Biome is distinct from the other biomes except for forest patches at higher rainfall levels. The Savanna Biome is distinct from the other biomes with the exceptions of forest patches at higher rainfall levels, the Grassland Biome, and an area representing Nama-Karoo invasion at lower rainfall levels (see Section 3.3). The Grassland Biome falls entirely within the moisture matrix domain of the Savanna Biome, has forest patches at higher rainfall levels and has an area representing invasion by Nama-Karoo (see Section 3.3) at lower rainfall levels. Forest patches, therefore, occur in the higher rainfall areas of the Fynbos, Savanna and Grassland Biomes.

TABLE 2.—Relative dominance in terms of percentage canopy cover for the life forms of selected vegetation units in each Biome

Vegetation units	Locality	Author	Biome	Phanerophytes	Hemicryptophytes	Chamaephytes	Therophytes	Geophytes	Relative dominance in terms of canopy cover (%)
<i>Stipagrostis ciliata</i> Community excluding drainage lines	Central Namib	Robinson (1976)	Desert	0,0	3,6	0,1	96,3	0,0	
<i>Ruschia cardyi</i> — <i>Pteronia paniculata</i> Association	Robertson Karoo	Olivier (1966)	Succulent Karoo	7,0	4,0	85,4	2,3	1,3	
<i>Trachypogon spicatus</i> — <i>Themeda triandra</i> Grassland	Eastern Orange Free State	Poigtier (1982)	Grassland	0,0	96,7	0,3	0,1	2,9	
Forest communities of the mist belt	Transvaal Drakensberg	Deall (in press)	Forest	86,9	8,8	4,1	0,0	0,2	
<i>Colophospermum mopane</i> — <i>Euclea divinorum</i> — <i>Enteropogon macrostachys</i> High Tree Savanna	North-eastern Transvaal Lowveld	Van Rooyen (1978)	Savanna	43,3	50,6	5,6	0,4	0,0	
<i>Hermannia coccocarpa</i> — <i>Nestleretum confertae</i>	Upper Orange River area	Wenger (1973)	Nama-Karoo	1,2	36,2	63,4	0,1	0,1	
Fynbos communities of the Swartboschkloof Nature Reserve	South-western Cape	Wenger, Kruiper & Taylor (1972)	Fynbos	35,2	28,1	33,5	0,0	3,2	

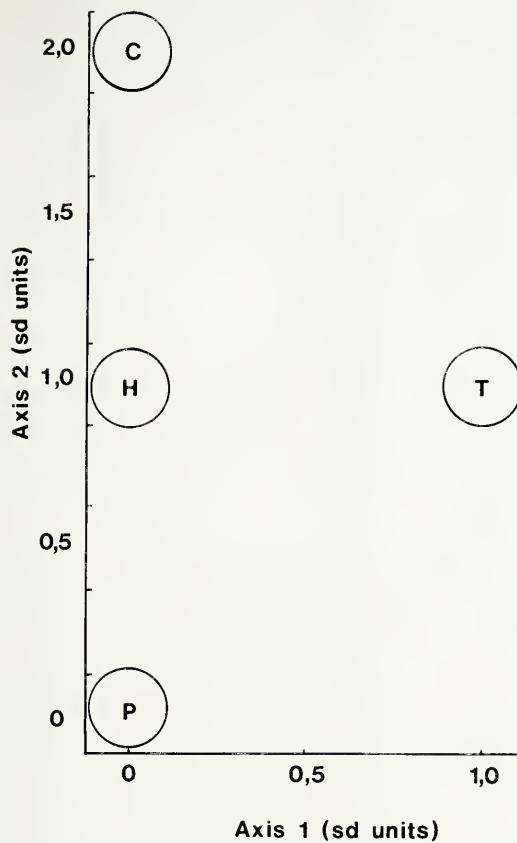


FIG. 9.—A detrended correspondence analysis ordination of life forms showing the separation of therophytes from the other life forms on the first axis. Abbreviations for life forms are: P, phanerophyte; Ch, chamaephyte; H, hemicyclopediae; and T, therophyte.

The Desert Biome in southern Africa is mainly limited to the summer and strong summer rainfall areas with greatest summer aridity (rainfall seasonality terms according to Bailey 1979, see Section 1.2.3). The Summer Aridity Index (SAI) does not fall below 5.0 in the strong summer rainfall area and not below about 6.5 to 7.5 towards the winter rainfall area. Maximum mean annual rainfall for this biome is approximately 85 mm but for most of the area, the mean is usually considerably less than 70 mm. Mean annual rainfall at the station with the lowest rainfall (No. 734/773, 22 year period) was 13.3 mm.

The Succulent Karoo Biome is mainly limited to the even, winter and strong winter rainfall areas with greatest summer aridity in southern Africa. Acocks (1975) states that his broad succulent karoo unit (Maps 1–4) ‘belongs in the winter rainfall area’. SAI does not fall below 4.8 to 5.2 in the even and winter rainfall areas and not below 5.3 to 6.0 in the strong winter rainfall areas. Maximum SAI was approximately 7.5. Mean annual rainfall ranged from approximately 20 to 290 mm.

The Nama-Karoo Biome is limited to strong summer, summer and even rainfall areas with SAI between approximately 3.6 and 5.1. In an area with less summer aridity (SAI as low as 3.1) in a summer and strong summer

rainfall area, Nama-Karoo overlaps with part of the Grassland and Savanna Biomes and is interpreted as an area of Nama-Karoo invasion (in the form of chamaephytes) for the following reasons:

- (1) it is not separated in terms of either the moisture matrix or temperature-moisture matrix (see below);
- (2) its delineation within the moisture matrix is of irregular shape which, in contrast to the area of Grassland, is not explained by the main alternative climatic factor of temperature. In a matrix with variables that are continuous and which are of prime relevance to biotic components concerned, niche shape tends to be fairly uniform. With anthropogenic plant invasions, the irregular shape can only be expected to become uniform when either the invasive elements return to their original niche or a new equilibrium is established between plant and climate;
- (3) the historical and direct evidence (*inter alia*, Acocks 1975), which clearly demonstrates invasion of, primarily, chamaephytes in these areas.

Mean annual rainfall for the entire biome ranges from approximately 100 to 520 mm. A disjunct area of the Nama-Karoo Biome occurs at lower SAI values of between approximately 2.4 and 2.9 in an area of strong summer rainfall. This area has not been plotted in Fig. 10 since data were available only from stations with records for six to ten years. This anomalous higher rainfall area is discussed in Sections 3.4 and 4.6.

Most of the Savanna Biome is limited to the summer and strong summer rainfall areas with SAI less than 4.0. However, an extension with predominantly succulent plant forms (Fig. 10, No. II), with mainly even rainfall and with higher summer aridity (SAI up to 5.0) occurs. This area is represented almost exclusively by a single Veld Type, namely No. 25 (Acocks 1975). Lowest mean annual rainfall is approximately 235 mm but in the succulent form area (Fig. 10, No. II) can drop to 185 mm. It is therefore clear that the Savanna Biome corresponds with a particular climate and it is misleading to state that no ‘savanna climate’ exists (Eyre 1963).

The Grassland Biome is limited to the summer and strong summer rainfall areas with SAI between 2.0 and 3.9. Mean annual rainfall is mostly between 400 and 2 000 mm. However, the moisture matrix does not differentiate the Grassland Biome satisfactorily and the temperature-moisture matrix (see below) is required. In contrast, another grassland type is differentiated in terms of the moisture matrix but it is possible that this rather limited area may also coincide with specific edaphic conditions. This area is strictly limited to summer and strong summer rainfall areas with SAI between 4.6 and 5.2 and with mean annual rainfall in the relatively narrow range of 70 to 100 mm and is therefore, appropriately termed arid grassland (Fig. 10). This area is not of biome dimension and is therefore not mapped (included in the Nama-Karoo mapping unit), but is of considerable interest relative to the mappable Grassland Biome. Similarly, Cain *et al.* (1959) indicate climatically disjunct grasslands, also separated by the

combination of hemicryptophytes and chamaephytes (Nama-Karoo). The area of arid grassland tends to be associated with sandy substrates. Leistner (1967) and Leistner & Werger (1973) observed in arid areas that, whereas compact soils have a high percentage of chamaephytes, sandy substrates have a high percentage of hemicryptophytes. Sand is important in separating grassland and dwarf shrubland in 'desert' regions (Tinley 1977). At low rainfall levels, the effect of the difference between sands and compact soils is explained in terms of infiltration and retention of water. Arid grassland is, distinguished in terms of moisture relations whereas mesic and hygric grasslands are distinguished in terms of temperature relations (see below).

The Fynbos Biome is limited to the strong winter, winter and even rainfall areas with SAI less than 6,0 in the strong winter area decreasing to about 3,0 in the even rainfall area. Mean annual rainfall ranges from about 210 to greater than 3 000 mm which is the largest range within a southern African biome. An area of climatic transition causes an irregular prominence (Fig. 10, No. I) in the demarcation of the Fynbos Biome. This area is represented almost exclusively by a single Veld Type, namely No. 43 (Acocks 1975).

The area indicated by I and II (Fig. 10) forms a central part of the moisture matrix and is surrounded by four biomes. Both areas I and II have several striking features in common. Each of these climatically defined areas contains almost exclusively single Veld Types. Each has a dominant life form category dominated by a single plant species, namely *Elytropappus rhinocerotis* (L.f.) Less. (Area I) and *Portulacaria afra* Jacq. (Area II), both of which belong to genera endemic to southern Africa. These peculiarities and other features have sometimes led to confusion in establishing the relationships of these areas with biomes. The alternative of creating a biome/s of these two areas is, with available data, inconsistent with the biome definition.

The Forest Biome in southern Africa is restricted to a single mappable unit in the even rainfall area. Forest patches occur in strong winter rainfall areas with SAI less than 5,1 and mean annual rainfall greater than 525 mm to strong summer rainfall areas with SAI less than 2,5 and mean annual rainfall greater than 725 mm. The forest formation identified with lowest mean annual rainfall in southern Africa occurs in the winter rainfall area (Taylor 1961). The lower limits given for forest do not apply to succulent forest patches (see Section 3.4).

Various other small areas of climatic anomaly are indicated in Fig. 10 and are discussed in Section 3.4.

At lower levels of summer aridity, all life forms are potentially dominant or codominant. As summer aridity increases, dominance or codominance of life forms is excluded at differing levels of SAI. Phanerophytic dominance or codominance is already excluded at lower levels of SAI and tends to vary quite considerably around a mean annual rainfall of about 235 mm (Fig. 10). Hemicryptophytic dominance or codominance is excluded at very different mean annual rainfall levels

depending on seasonality, but corresponds to a more limited range of SAI generally between 5,0 and 5,5. Chamaephytic dominance or codominance is excluded at greatly varying levels of both mean annual rainfall and SAI. The chamaephytic and hemicryptophytic dominance or codominance exclusion lines intersect in the summer rainfall area thereby reversing the order of exclusion for these two life forms. This may also relate to the edaphic conditions of the arid grassland mentioned above. No exclusion line for therophytic dominance exists at upper SAI levels in the moisture matrix. The phanerophytic dominance or codominance exclusion line in the winter rainfall area is discontinuous and displaced owing to the transitional nature of this part of area No. I (Fig. 10) in terms of mean height of renewal buds. Where life form dominance or codominance exclusion lines coincide, this does not necessarily imply that each of the two are equally excluded as non-dominants or non-codominants. The limits of life form dominance or codominance are discussed in more detail in Section 5.

The selected world stations (Fig. 10) indicated both correspondence and non-correspondence with southern African biomes thereby confirming that complete biome comparisons should be limited within continental and subcontinental areas. For areas with mean annual rainfall exceeding about 3 000 mm, forest is generally found. The selected world stations also indicate the approximate world range of the moisture matrix. The largest empty domain is for an area with extremely low values of SAI and strong summer rainfall, widening with increasing winter rainfall. Unrealistically high mean annual rainfall (tens of thousands of millimetres) would be required to occur in this domain. The slopes of the mean annual rainfall isolines are an automatic consequence of the expression of seasonality. Two other empty domains are those at positions of extreme rainfall seasonality, that is, about 2% away from 100% and 0%. It is noteworthy that, relative to the world data set, the southern African data set accounts for most of the range in the moisture matrix with the exception of the most extreme world values.

The ordination of biomes (Fig. 11) confirms the relationship between biomes and mean annual rainfall on both axes. The first axis separates irregular rainfall (Desert) from more regular rainfall (the other biomes) while the second axis forms a moisture gradient from Forest through Savanna and Nama-Karoo to Succulent Karoo but with Fynbos and Grassland covering most of the range. This parallels the ranges of plant production in the respective biomes (see Section 4).

Mean annual rainfall also affects the incidence of fire. Fire incidence usually increases above 235 mm mean annual rainfall and does not normally occur in areas below this value. Thus fire is prevalent in the Savanna, Grassland and Fynbos Biomes. In the last mentioned biome, both canopy and surface fires occur owing to the continuous structure of the vegetation and its high flammability, and fire frequency is generally not

## LEGEND

- Biome border
- Mean annual rainfall
- Upper SAI limit for forest patches
- - - Grassland Biome border
- X X X Limits of Nama-Karoo invasion of Grassland Biome
- x x x Limits of Nama-Karoo invasion of Savanna Biome
- Lower SAI limits of areas I and II
- ..... Apparent anomalies
- PPP Upper SAI limit of phanerophytic dominance
- CCC Upper SAI limit of chamaephytic dominance
- H H H Upper SAI limit of hemicryptophytic dominance

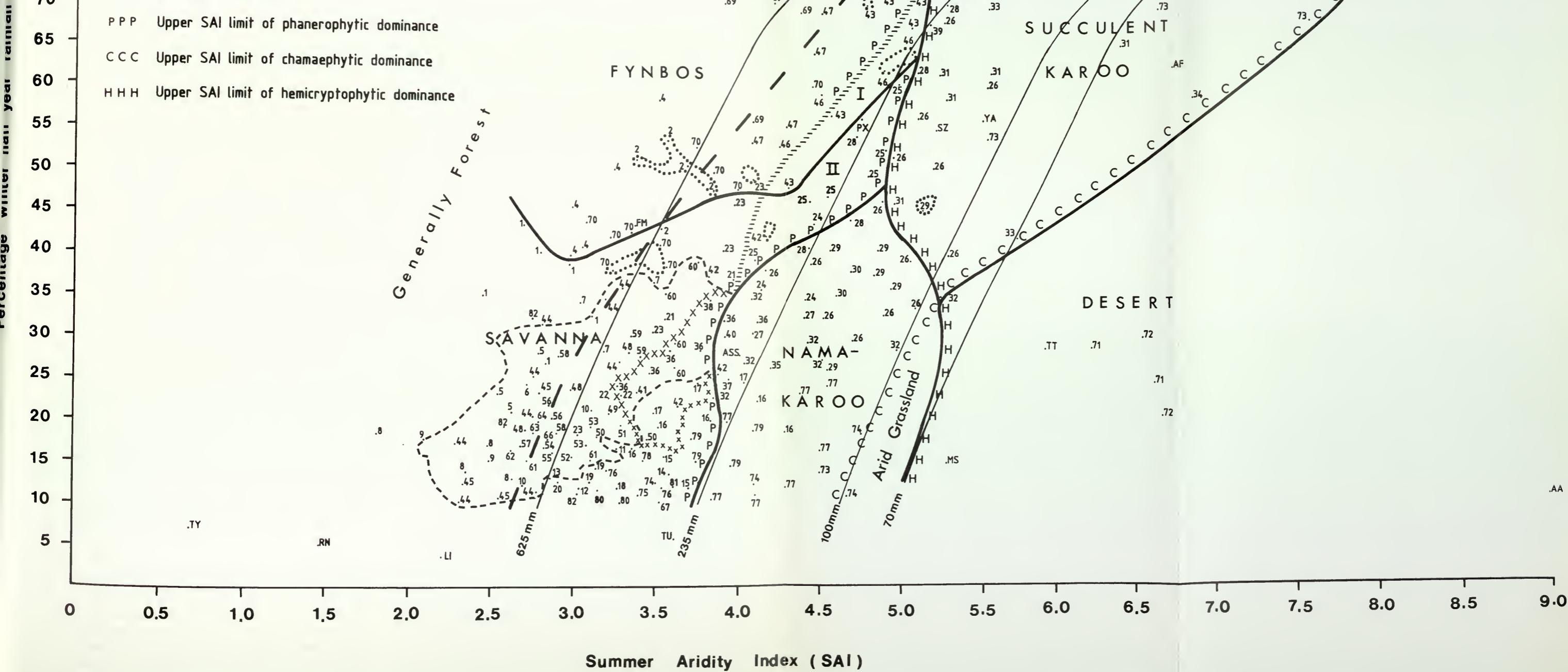
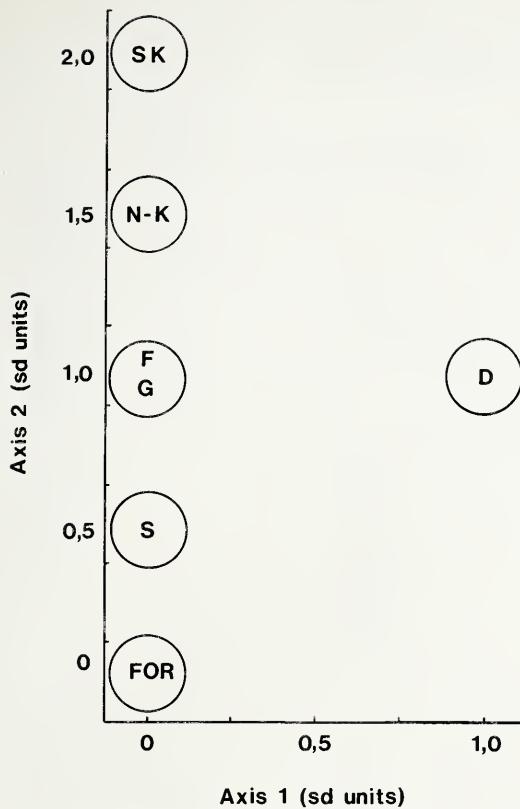


FIGURE 10.—The relation of biomes to a moisture matrix of the Summer Aridity Index (SAI) and percentage winter half-year rainfall showing: biome delimitation and name; plant invasions of biome proportions; apparent anomalies; upper SAI limits of dominance of life forms and selected mean annual rainfall isolines. Area I is Acocks's (1988) Mountain Renosterveld and area II is his Spekboomveld (or Succulent Mountain Scrub). Plotted points are selected (XX% of total used—see Appendix 1) climate stations for known dominant life form combinations and are numbered according to recognized vegetation types in which they occur. (Necessary divisions of some of these vegetation types across biome borders are discussed in Section 3.4.) Nos 1–70: Acocks's (1988) Veld types for South Africa, Lesotho and Swaziland; no representative stations were available for Nos 3, 31 (Willowmore–Steylerville section) and 68. Nos 71–79 correspond to Giess's (1971) vegetation types for Namibia; 71, Giess's type No. 2; 72, No. 3; 73, No. 3a; 74, No. 4; 75, No. 7; 76, No. 8; 77, No. 9; 78, No. 12; and 79, No. 13. Botswana, Zimbabwe and Mozambique stations are represented by Nos 80, 81 and 82, respectively. Selected world climatic stations are: AA, Arica (Chile); AF, Aoulef (Algeria); ANA, Antofagasta (Chile); AS, Algiers (Algeria); ASS, Alice Springs (Australia); CO, Cairo (Egypt); Ce, Orkvice (Yugoslavia); JM, Jerusalem (Israel); LE, Libreville (Gabon); LI, Lubumbashi (Zaire); MS, Mossamedes (Angola); PH, Perth (Australia); PX, Phoenix (USA); RN, Rangoon (Burma); SO, San Diego (USA); SZ, Santa Cruz (Argentina); TT, Tamanrasset (Algeria); TU, Timbuktu (Mali); TY, Tavoy (Burma); and Ya, Yuma (USA).

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**Axis 1 (sd units)**

FIG. 11.—A detrended correspondence analysis ordination of biomes showing the separation of Desert from other biomes on the first axis and separation of the other biomes on the second axis which corresponds to a moisture gradient. Abbreviations for biomes are: SK, Succulent Karoo; N-K, Nama-Karoo; F, Fynbos; G, Grassland; S, Savanna; FOR, Forest; and D, Desert.

less than four years. In the other biomes, surface fires prevail where hemicryptophytes form the main finely divided fuel load. Since the hemicryptophytic fuel load is usually positively correlated with mean annual rainfall (Rutherford 1980), the frequency of fire tends to increase in higher rainfall areas. Hemicryptophytic production decreases with dilution or overtopping by phanerophytes in Savanna. It follows that greatest frequency of fire is expected in the wetter parts of the grassland biome where annual fires are possible.

Although the moisture matrix does not differentiate the Grassland Biome (not arid grassland) satisfactorily from the Savanna Biome, the temperature–moisture matrix (Fig. 12) does provide such separation in terms of minimum temperatures and summer rainfall. This separation is determined by the exclusion of phanerophytic dominance in the moist and low temperature minimum areas (for details, see Section 5.1). Another pair of biomes that also clearly separates in terms of temperature minima and summer moisture is Succulent Karoo and Nama-Karoo. The Desert and Fynbos Biomes are also separated but mainly in terms of the summer moisture axis. In southern Africa, several biomes are not clearly distinguished in terms of this matrix. Major overlap occurs between

Desert and Succulent Karoo, Fynbos and Savanna, and Fynbos and Succulent Karoo. Forest patches overlap with Fynbos and Savanna at higher moisture levels but in Grassland, the microclimate of forest patches may be warmer than the surrounding grassland.

The partial overlap of Nama-Karoo and Grassland found in the moisture matrix (Fig. 10) corresponds to the overlap of these biomes in the temperature–moisture matrix and substantiates the interpretation of this area as invasion of Grassland by Nama-Karoo elements. Data for the disjunct higher rainfall area of the Nama-Karoo Biome referred to above, are not plotted for similar reasons (see also Sections 3.4 and 4.6).

Four biomes occur at higher temperature minima [ $>2^{\circ}\text{C}$ : mean lowest minimum temperature for coldest month — (LMN)], namely, Savanna Fynbos, Succulent Karoo and Desert. Only Desert is entirely above  $0,0^{\circ}\text{C}$  (LMN). At a lower range of temperature minima ( $0^{\circ}\text{C}$  to  $-3^{\circ}\text{C}$ ) parts of all biomes, except Desert, occur. At extreme temperature minima ( $<-9^{\circ}\text{C}$ ) parts of only Nama-Karoo and Grassland occur. Although the altitude of parts of Fynbos is similar to that of these two biomes, extreme temperatures are rare because of the ameliorating effect of rainfall in the cold season. Savanna has the greatest range of temperature minima (see Section 5.1).

### 3.3 Intra-biome interactions

Interactions between life forms within biomes include competition for resources and interactions influenced by fire, wood removal and grazing. The outcome of these interactions determines which life form/s is/are dominant within a biome. This section considers some of the effects of interactions and the relative success of life form components within each biome. Each potential combination of two life forms appropriate to each biome is discussed, firstly where the dominance of the one life form is excluded and secondly where they both coexist. Further discussion on specific ecological and environmental relationships of dominant life forms is contained in Section 5.

The following main patterns of interaction between phanerophytes and chamaephytes at biome scale are suggested. In the Forest Biome, chamaephytic dominance is excluded where phanerophytes, by virtue of size, tend to dominate the available resource space. In the Savanna Biome, chamaephytic dominance is also excluded, but probably not primarily by action of phanerophytes but by that of hemicryptophytes (see below). An ancillary effect in excluding chamaephytic dominance is that of prevalent surface fires which tend to disadvantage chamaephytes relative to phanerophytes. In the Nama-Karoo and Succulent Karoo Biomes, phanerophytic dominance is excluded probably because low water supply levels are adequate for only the chamaephytes (and for hemicryptophytes in the Nama-Karoo Biome). By contrast, in the Fynbos Biome, phanerophytes and chamaephytes are codominant. In the Fynbos Biome, the phanerophytic dominants are generally much smaller

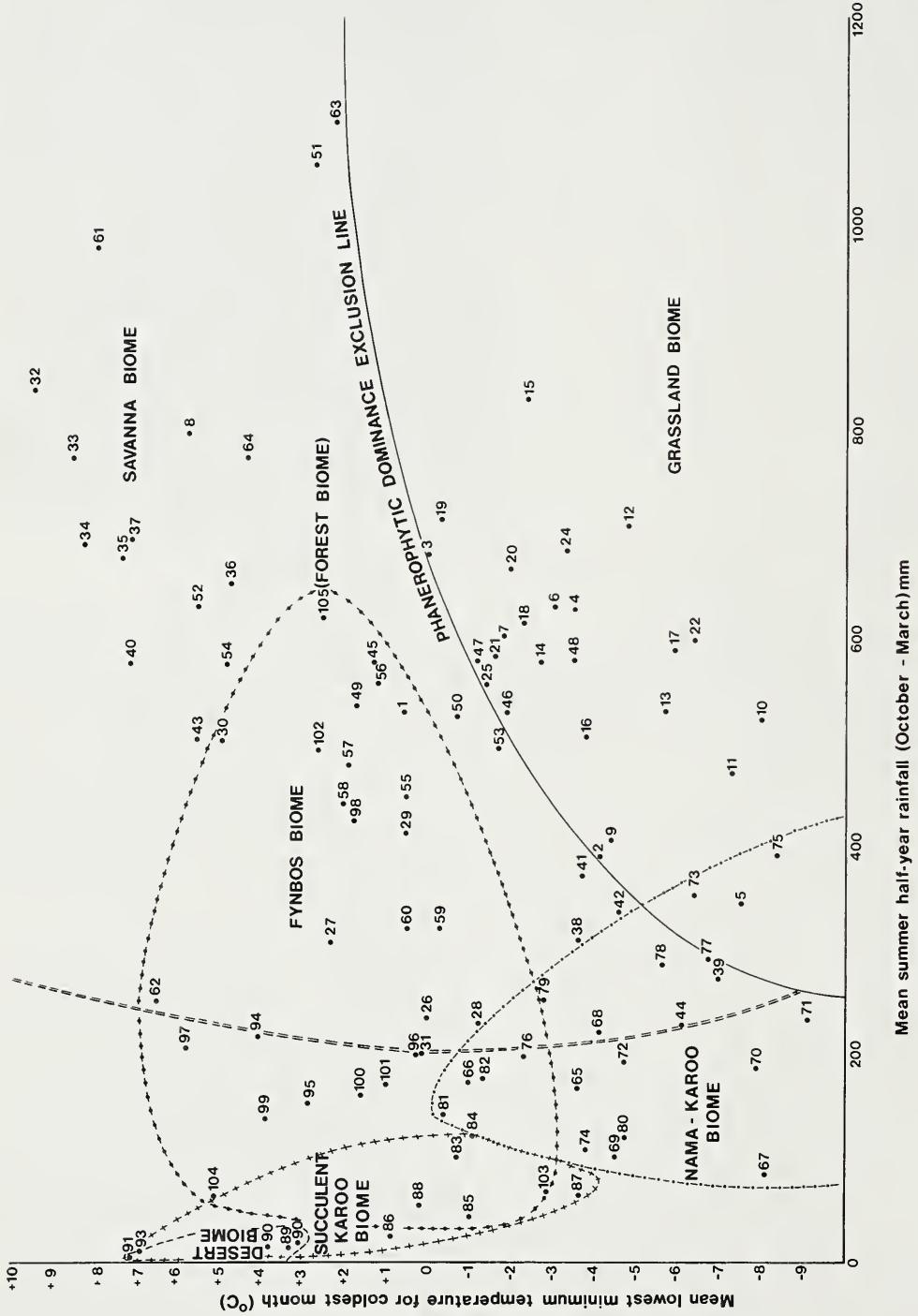


FIG. 12.—The relation of biomes to a temperature – moisture matrix of mean summer half-year rainfall and mean lowest minimum temperature for the coldest month. Climate stations used are numbered and fully referenced in Appendix 2. Biome borders are approximate because of few available data points. The Forest Biome is parenthesized because it is represented only by a single point (105). The lower rainfall limit of the Savanna Biome is indicated by a double dashed line. Other biome borders are self-evident.

than in the other biomes which, together with their leaf size and orientation, tends to leave a relatively greater resource space available for other life forms. Fire is detrimental to both life forms.

The following main patterns of interactions are suggested between phanerophytes and hemicryptophytes. In the Forest Biome, hemicryptophytic dominance is excluded for the same reasons as for the exclusion of chamaephytic dominance. In the Grassland Biome, the exclusion of phanerophytic dominance is associated with temperature minima too low for effective establishment of phanerophytes (see Section 5.1). An ancillary factor that reinforces this exclusion is surface fire. By contrast in both Savanna and Fynbos Biomes, phanerophytes and hemicryptophytes are codominant probably due to spatial partitioning of resources. Walter (1979) explores the implications of such partitioning in savanna vegetation. He refers to the existence of a labile equilibrium between grasses (hemicryptophytes) and woody plants (mainly phanerophytes). In arid areas, rainfall is insufficient to penetrate through the grass rooting zone to that of the woody plants so that grasses are dominant. With increasing rainfall, more water does penetrate through to the woody plant rooting zone so that, although grasses remain dominant, woody plants increase. At a certain level of higher rainfall, shading by the more abundant trees reverses the competitive relationship. This point of equilibrium is labile and can be moved in either the direction of the grasses or trees. Utilization of grasses (mainly through grazing) results in increased availability of water to the woody plants, which is advantageous to the latter. Over-utilization results in woody plant encroachment and grass can decline to levels insufficient for intense fires that are needed to help counteract the woody plants (Trollope 1984). During the long term lower rainfall periods, disproportionately less water may penetrate through the grass rooting zone to that of the woody plants, which is detrimental to the latter.

The following main patterns of interactions between chamaephytes and hemicryptophytes are suggested. In the Savanna and Grassland Biomes, chamaephytic dominance is excluded probably because grasses effectively dominate the potential chamaephytic resource space. A contributory factor in this exclusion is surface fire. In the Succulent Karoo Biome, hemicryptophytic dominance is excluded where summer aridity is too extreme for hemicryptophytic dominance but not for chamaephytic dominance, especially that of succulents. Past grazing practices may have contributed to this exclusion but reliable evidence appears lacking. By contrast, in the Fynbos and Nama-Karoo Biomes, hemicryptophytes and chamaephytes are codominant and this may be linked to the temporal partitioning of resources. Evidence suggests that in Nama-Karoo, growth of hemicryptophytes is mainly in summer whereas that of chamaephytes is generally outside summer (Roux 1966; Vorster & Roux 1983). The growth phase of life forms in the Fynbos Biome is scattered through much of the year (Pierce 1984), which

suggests temporal resource partitioning between various life forms in this biome.

In the interaction between geophytes and hemicryptophytes in the Grassland Biome, it has been shown that geophytes are often excluded when fire and grazing are also excluded (Tainton & Mentis 1984). This may also apply to parts of the Fynbos and Savanna Biomes.

Therophytes have poor competitive ability in all biomes except the Desert Biome where dominance of other life forms are excluded by climate. Although therophytes can be fairly common in parts of the Succulent Karoo, they decrease along the increasing moisture gradient (Fig. 11), which corresponds with the increasing degree of competition with perennial plants to the Forest Biome. Despite the large number of therophytes in Succulent Karoo, the vegetation has 'a decided chamaephytic character' (Van Rooyen *et al.* 1979).

Through manipulating the competitive balance between dominant life forms, parts of a biome may be transformed to another. There are several examples of such transformations. These transformations are not climatically induced but are anthropogenic.

In the Grassland Biome, when over-utilization of hemicryptophytes reduces the hemicryptophytic dominance of the resource space, chamaephytes can then become codominant, thus effecting a transformation to Nama-Karoo. It has been demonstrated that this type of transformation can occur at biome scale (see Section 3.2) and has led to, what Acocks (1975) terms, the most spectacular of all the changes in the vegetation of South Africa. It is interesting to note that in this area, rainfall appears to have been lower during more recent decades than during earlier parts of this century.

Another example is the transformation of Savanna to Grassland. Here, the sustained removal of woody plants for fuel or structural purposes favours the hemicryptophytes, thus effecting a transformation to Grassland. What is regarded as marginal grassland on the eastern seaboard of South Africa is potentially savanna, whereas what is regarded as marginal savanna could, under continued woody plant removal and assisted by fire, become Grassland.

The transformation of Savanna to Forest is possible but is usually limited to sub-biome scale areas of bush encroachment through over-utilization of the hemicryptophytes (see above). With conservation management, a limited increase in the extent of Forest is possible in areas with savanna structure along the eastern seaboard. In certain areas, changes from marginal grassland to Forest can occur via an albeit transitory, savanna-structure vegetation.

### 3.4 Spatial relationships

The seven biomes of southern Africa are delineated at biome scale in Fig. 13. The Savanna Biome is largest and comprises 46.16% of southern Africa (Table 3). It occurs in east-central South West Africa/Namibia, in almost all of southern Botswana, most of the northern

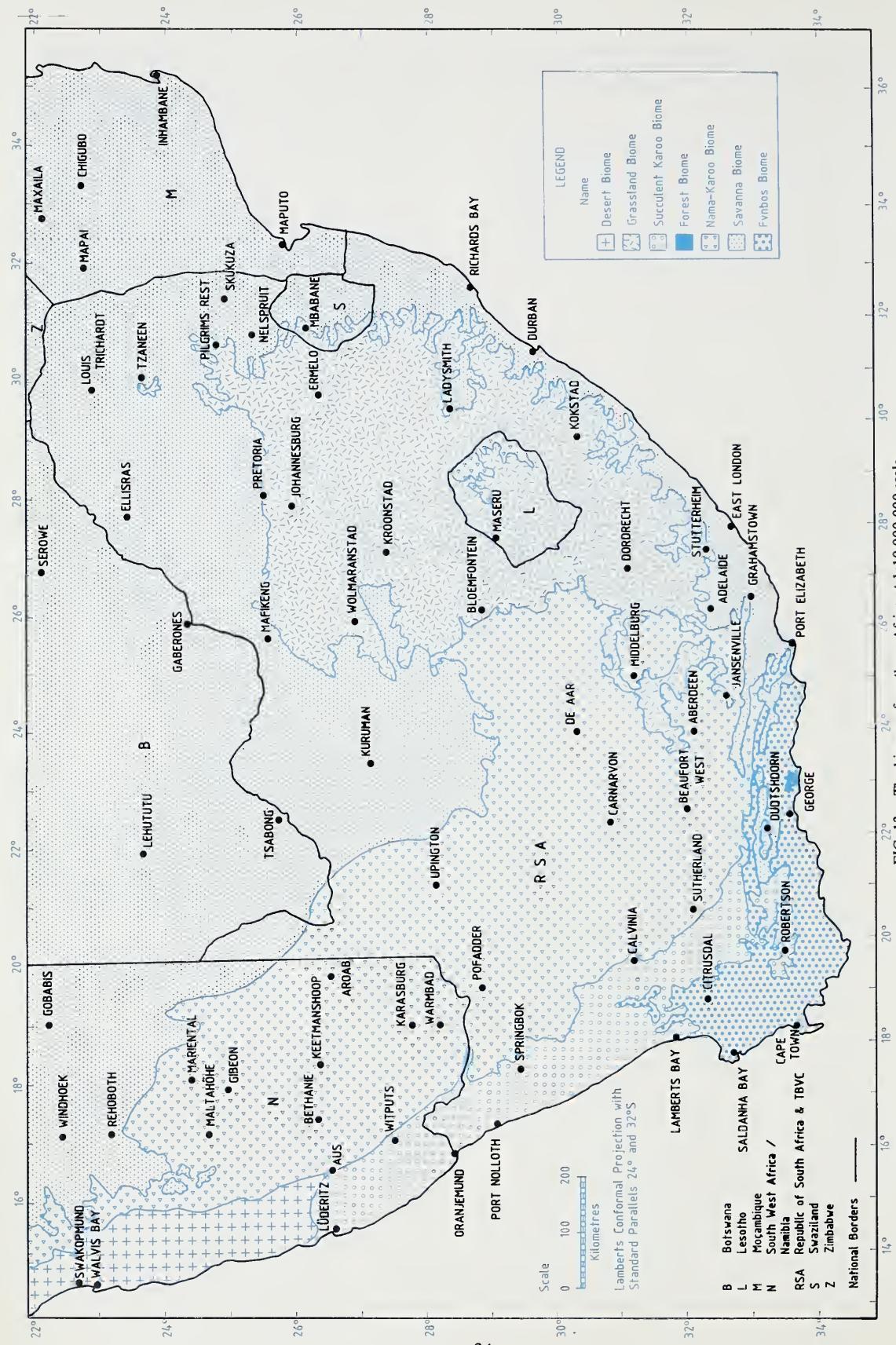


FIG. 13.—The biomes of southern Africa at 1:10 000 000 scale.

TABLE 3.—Areas\* of the Biomes in southern Africa south of 22°S

	Savanna km <sup>2</sup>	%	Nama-Karoo km <sup>2</sup>	%	Grassland km <sup>2</sup>	%	Succulent Karoo km <sup>2</sup>	%	Fynbos km <sup>2</sup>	%	Desert km <sup>2</sup>	%	Forest km <sup>2</sup>	%	Total km <sup>2</sup>	%
Republic of South Africa & TBVC**	408 876	33,49	346 107	28,35	313 962	25,71	81 908	6,71	69 875	5,72			309	0,02	1 221 037	100
Lesotho	13 993	79,28	5 145	16,74	25 598	83,26							30 743	100		
Swaziland	102 804	27,58	187 791	50,37	3 656	20,72	29 304	7,86					17 649	100		
South West Africa/Namibia	287 198	99,28	2 084	0,72					52 893	14,19			372 192	100		
Botswana	5 302	100,00											289 282	100		
Zimbabwe	140 894	100,00											5 302	100		
Total (south of 22°S)	959 667	46,16	541 127	26,05	343 216	16,52	111 212	5,35	69 875	3,36	52 893	2,55	309	0,01	2 077 699	100

\* Calculated according to the cut and weigh method at 1:1 500 000 scale

\*\* Republics of Transkei, Bophuthatswana, Venda and Ciskei

Cape Province, most of the northern two-thirds of Transvaal, central and eastern Swaziland, all of southern Mozambique, the lower altitude belt of the eastern seaboard of Natal and the eastern Cape Province. Savanna Biome outliers (outliers here always refer to those mappable at biome scale) occur on the southward extent of the western escarpment in South West Africa/Namibia, and isolated areas of Spekboomveld\* in the south-eastern and southern Cape Province. The last-mentioned outliers of savanna in the Cape are determined on life form criteria and are, in terms of the moisture matrix (Fig. 10), an extreme form of savanna. Because of the close affinity between Spekboomveld\* and Valley Bushveld of the eastern Cape Province, discussion of this extreme savanna is included in the discussion of affinities of Valley Bushveld (below).

The second largest biome is the Nama-Karoo Biome comprising 26,05% of southern Africa (Table 3). It extends in a belt from the eastern Cape Province interior, through most of the central Cape Province and Nama-land, narrowing to a northward extension at the base of the escarpment in South West Africa/Namibia. This narrow portion includes unmappable arid grassland and the karroid shrub communities referred to by Heydorn & Tinley (1980). Patches of arid grassland are found southwards along the most arid (western) margin of the Nama-Karoo Biome in South West Africa/Namibia and in parts also associated with a sand veneer (Heydorn & Tinley 1980) in Bushmanland, South Africa. Parts of arid grassland in Bushmanland are dominated by the grass species *Stipagrostis brevifolia* (Nees) De Winter which is less hemicryptophytic than it is chamaephytic. A higher rainfall outlier of the Nama-Karoo Biome occurs at high altitudes almost exclusively in north-eastern Lesotho. Largely owing to floristic distinction, this area has not normally been included in a karroid biome. The vegetation has a karroid physiognomy (see Fig. 4,12, Killick 1979) with codominance of dwarf shrubs and grasses (Martin 1984). Van Zinderen Bakker (1981) refers to a 'Karoo type of vegetation ... locally known as 'Sehalahala' in the high mountains of Lesotho'. In these areas '*Chrysocoma tenuifolia* an invader from the Karoo is common' (Killick 1979). In high mountains, rainfall varies inversely with altitude (Killick 1978b) so that the summit areas of the Drakensberg experience altitudinal drought (Killick 1963). An approximate reduction of 50 mm in rainfall per 300 m increase in elevation above 1600 m is expected in Lesotho. Since most of the biome outlier lies on the leeward side of the escarpment, a rain shadow prevails (Killick 1978b) and even at altitudes in excess of 3 000 m, mean annual rainfall can be as low as 634 mm (Killick 1979). At these elevations, rainfall can also be rendered less effective through observed physiological drought (Killick 1963) and many plants exhibit xeromorphic features (Herbst & Roberts 1974).

The Grassland Biome covers 16,52% of southern

Africa, It is found mainly on the high central plateau of southern Africa, inland areas of the seaboard of Natal and mountains of the south-eastern Cape Province. An outlier of this biome occurs on a portion of the north-eastern Transvaal escarpment (Rutherford & Westfall 1984).

The Succulent Karoo Biome covers 5,35% of southern Africa (Table 3) and is found in the western Cape Province coastal areas, Namaqualand, south-western Cape interior and south-western coastal area of South West Africa/Namibia. Outliers of this biome occur in the little Karoo and Robertson Karoo.

The Fynbos Biome covers 3,36% of southern Africa (Table 3) and occurs in the south-western and southern Cape Province. Outliers occur on inland ranges of the Cape folded mountain belt and at the northern and eastern extremities where arid corridors sever the extensions.

The Desert Biome covers 2,55% of southern Africa, but it should be noted that most of the area of this biome falls outside the defined area of southern Africa. No outliers of Desert Biome are evident.

The Forest Biome covers 0,01% or 309 km<sup>2</sup> of southern Africa and is limited to the southern Cape Province at biome scale (see Section 2.2 for difficulties in delineation). The area of this biome together with all forest patches elsewhere (in areas of the Grassland, Savanna and Fynbos Biomes) is 2 000 to 3 000 km<sup>2</sup> (C.J. Geldenhuys pers. comm.). The mapped Forest Biome, therefore, represents only 10,3 to 15,5% of the area of all forest patches. Unmappable outliers of other biomes include the south-western extension of savanna into the Robertson Karoo as bush clumps, or the therophytically dominated anthropogenically disturbed areas 'deserts' of various biomes. In contrast to the Forest Biome, the inclusion of such unmappable outliers would not affect relative areas of the biomes significantly.

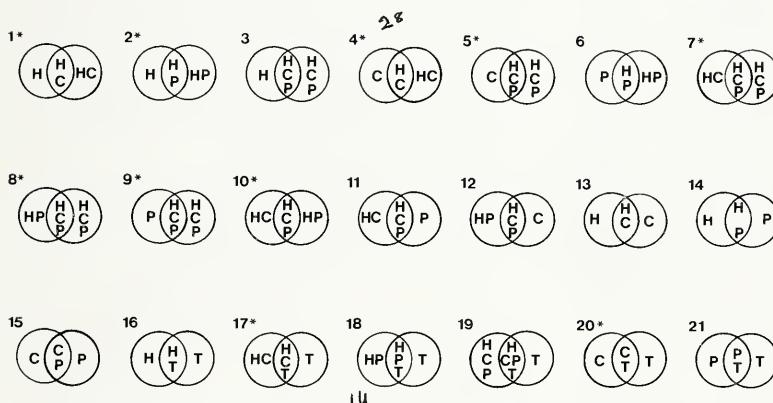
At interfaces between biomes, dominant life forms from the adjacent biomes can form different combinations to that of either biome. Non-dominant life forms from either of the two adjacent biomes do not become dominant at the interface of biomes because their climatic exclusion of dominance still applies. The 21 theoretically possible combinations of life forms at biome interfaces are given in Fig. 14 (excluding geophytes). Eleven of these interfaces do not occur at biome scale (Fig. 13) and the combinations are therefore irrelevant at this scale. One of these, however, may be construed as constituting a whole biome, namely the Nama-Karoo Biome being the interface area between chamaephytic dominance (Succulent Karoo Biome) and hemicryptophytic dominance (Grassland Biome). In the Nama-Karoo Biome there is a gradation from the Succulent Karoo Biome to the Grassland Biome in terms of rainfall, frost, rainfall seasonality, fire frequency, grass cover and abundance of succulents. This gradation is paralleled by changes in the relative importance of photosynthetic pathways of plants (Werger & Ellis 1981). The remaining 10 biome interfaces may be grouped into:

\* Veld types refer to those of Acocks (1975).

1, those with *no* interface area of different life form combinations to that in *one* of the adjacent biomes, and

2, those *with* an interface area with different life form combinations to those in both of the adjacent biomes.

There are seven interfaces in the first group: Grassland and Nama-Karoo; Grassland and Savanna; Succulent Karoo and Nama-Karoo; Succulent Karoo and Fynbos; Nama-Karoo and Fynbos; Savanna and Fynbos; and Forest and Fynbos. In these combinations the theoretical interface area is identical in composition to the adjacent biome with greater number of life forms and is therefore redundant and borders are conceptually straightforward.



The three interfaces of the second group are those of the Nama-Karoo and Savanna, Nama-Karoo and Desert, and Succulent Karoo and Desert Biomes. The interface areas of the last-mentioned two biome pairs involve therophytic codominance. These areas are unmappable at biome scale with the available information and the border lines between the biomes run through the interface areas. The combination of Nama-Karoo and Savanna Biomes can result in areas of codominance of hemicryptophytes, chamaephytes and phanerophytes and may be termed 'pseudo-fynbos' on the basis of structure and its relation to climate. This interface area of often patchy 'pseudo-fynbos' complicates the drawing of parts of the border between Nama-Karoo and Savanna Biomes. In the eastern Cape Province, this problem applies particularly to parts of the False Karroid Broken Veld and Valley Bushveld. These interface areas contribute to the confusion in vegetation patterns in the eastern Cape Province. In parts of the northern Cape Province, South West Africa/Namibia and Botswana in the parallel dune areas of the southern Kalahari, the karoo shrub complex does not survive effectively on the Kalahari sand surface (Barker 1983). In this area, the Nama-Karoo of the compacted soils of the interdune areas and the Savanna of the dunes merge at biome scale to form 'pseudo-fynbos', the ratio of these two substrates together with climate govern the delineation between these two biomes.

Various anomalies in the relation of climate to biomes occur for specific areas of southern Africa (Fig. 10). In the moisture matrix's Fynbos Biome area, four

anomalous areas have been identified:

1, an area of Mountain Rhenosterbosveld (Veld Type 43) which is physically outside the Fynbos Biome on the Roggeveld escarpment between the Succulent Karoo and Nama-Karoo Biomes and in the Karniesberg area in the Succulent Karoo Biome. These limited areas contain vegetation different to the surrounding biomes and are only marginally similar in vegetation structure to that in the Fynbos Biome but show some floristic affinity with the Fynbos Biome (Oliver *et al.* 1983). The life form combinations nevertheless preclude this area from being considered as part of the Fynbos Biome. The relation between combinations of life form dominance and

FIG. 14.—Set diagrams illustrating the possible dominant life form combinations at biome interfaces. H, hemicryptophyte; C, chamaephyte; T, therophyte and P, phanerophyte. Nos. 1–9 do not have interface areas (the potential interface area is the same as one of the adjacent sets). Nos. 10–21 have interface areas distinct from the adjacent biomes. Asterisks indicate existence of interfaces at biome scale.

climate is subject to the effect of palaeoclimate. Such anomalies may be attributed to the fact that the life form combinations have not yet adapted to current climate;

2, a very limited occurrence (in part of the southern belt) of Coastal Rhenosterbosveld (Veld Type 46) in the Mountain Rhenosterbosveld (Veld Type 43) area of the moisture matrix. In view of its particularly low rainfall, it can be presumed to be equivalent to Mountain Rhenosterbosveld;

3, the occurrence of Valley Bushveld (Veld Type 23) — represented by a single site — in the Fynbos Biome area on the moisture matrix. This site is in close proximity to the Fynbos Biome in the eastern Cape Province, and may be considered marginal savanna;

4, the Alexandria Forest (Veld Type 2) has been recognized as anomalous with regard to climate (Marker & Russell 1984). This forest area does not have a sufficient water surplus to account for the existence of forest without recourse to a mist input which is a significant factor in the survival of this marginal forest (Marker & Russell 1984). The marginal nature of Alexandria Forest is also indicated in that this veld type straddles the limit of lowest rainfall necessary for the occurrence of forest patches (Fig. 10). These limitations result in forest units that are unmappable at biome scale. In the drier parts, Alexandria Forest is replaced by savanna and in the wetter parts by grassland (Acocks 1975). These grassland areas can have strong Fynbos affinities (Acocks 1975), which accords with the position of this area on the moisture matrix (Fig. 10). When the whole unit

(Veld Type 2) is viewed in perspective, it is clear that phanerophytes and hemicryptophytes are codominant and the area is consequently mapped as part of the Savanna Biome.

In the area represented by the Savanna Biome on the moisture matrix (Fig. 10), two areas of anomaly have been identified. One of these areas is that of False Macchia (Veld Type 70) at the extreme eastern extension of this veld type on the Suurberg and in the Grahamstown vicinity. Although this area is traditionally considered part of the Fynbos Biome, based mainly on floristics and correlation with stratigraphy, its life form combination does not satisfy the requirements of the Fynbos Biome, but that of Savanna. This area can have an almost exclusive grass understorey to the proteoid overstorey (Moll & Jarman 1984b). The area in question is, therefore, not anomalous within the present study and is fully consistent within the moisture matrix relations (Fig. 10). The second anomalous area is an isolated patch of Karroid *Merxmuellera* Mountain Veld replaced by Karoo (Veld Type 42) on the eastern Nuweveld Escarpment within the Nama-Karoo Biome. Although Acocks (1975) indicates that the grass component is important in this area, he also points out that it has many karroid and rhenosterbosveld affinities with taller plants. This area falls within that part of the moisture matrix (Fig. 10), represented by the marginal savanna type — Spekboomveld (Veld Type 25). The heterogeneous combinations of life forms may relate to the presence of a 'savanna climate' (in terms of moisture but not necessarily temperature) in the Nama-Karoo Biome which is reminiscent of 'pseudo-fynbos' discussed above.

In the Succulent Karoo Biome part of the moisture matrix (Fig. 10), an anomalous part of the Arid Karoo (Veld Type 29) occurs. This small area is in the south-western sector of the area south of the Calvinia-Carnarvon line which, although mapped as part of the Nama-Karoo Biome, is likely to come close to satisfying the criteria for the Succulent Karoo Biome. Acocks (1975) names this area the Semi-succulent Southern Form of Arid Karoo in which 'mesembs' are more plentiful than grasses. Adequate data for this particular area are lacking. It should be stressed that all the above anomalies together constitute a very small proportion of the total area of southern Africa.

Although many of the Biome borders follow those of the Veld Types of Acocks (1975) (Table 4), several Veld Types had to be divided because of different dominant life form combinations within the same Veld Type (Table 5). These divisions were often identified in Acocks's (1975) text subdivisions or forms, or alluded to less directly. It was often necessary to disregard Acocks's explicit and any implicit groupings of Veld Types. In South West Africa/Namibia there was usually greater discrepancy between biome borders and the vegetation type borders of Giess (1971).

The difficulty in determining the border between the Forest and Fynbos Biome owing to irregular shape

and patchiness, has been discussed in Section 2.2. The 'Knysna Forest' (Veld Type 4) of Acocks (1975) bears little resemblance to the actual occurrence of forest. The only Veld Type that required dividing between the Fynbos and Savanna Biomes, was False Macchia (Veld Type 70) at its eastern extremity (see above). The isolated patches of Valley Bushveld in the southern part of the Fynbos Biome area could not be mapped at biome scale. Similarly, a narrow zone of savanna that occurs between the Fynbos and Nama-Karoo Biomes and which is also suggested by the biome relationships in the moisture matrix (Fig. 10), is unmappable. To fully distinguish between the Fynbos and Succulent Karoo Biomes, it was necessary to divide Strandveld (Veld Type 34) and Mountain Rhenosterbosveld (Veld Type 43). In Strandveld, there is a very gradual gradient of changes in life form combinations from that corresponding to the Fynbos Biome (Boucher & Jarman 1977) to that which is clearly Succulent Karoo Biome. This type of gradient made border determination difficult. Available climatic data supported Kruger's (1979a) division of this Veld Type at Elands Bay. This delimiting point was accepted.

Mountain Rhenosterbosveld (Veld Type 43) posed one of the greatest problems in the allocation of Veld Types to biomes because the dominant species often straddles the chamaephyte–phanerophyte height limit. Where Mountain Rhenosterbosveld was contiguous with fynbos, hemicryptophytes were well represented (Van Rensburg 1962) and the dominant life form combination approximated that of the Fynbos Biome. This qualifies Taylor's (1978) and Kruger's (1979a) total exclusion of Mountain Rhenosterbosveld from the Fynbos Biomes (or its equivalent). Where Mountain Rhenosterbosveld was not contiguous with Fynbos, the dominant life form combinations tended to exclude such areas from the Fynbos Biome (see above). The latter areas of Mountain Rhenosterbosveld occur in the Succulent Karoo and Nama-Karoo Biomes. Despite the differences between these areas and the vegetation of the surrounding biomes, the Mountain Rhenosterbosveld areas that were contiguous with Succulent Karoo were included in this biome; those that were contiguous with the Nama-Karoo Biome were included therein. The Mountain Rhenosterbosveld included in the Succulent Karoo Biome is a possible contender for a chamaephyte–phanerophyte codominant biome (in addition to the existing seven biomes — see Fig. 8) but the status of such a biome would be extremely marginal. Coastal Rhenosterbosveld (Veld Type 46) is, in contrast to Mountain Rhenosterbosveld, widely accepted as part of the Fynbos Biome (for example, Taylor 1978; Kruger 1979a), is non-karroid in affinity (Acocks 1975) and is floristically closely related to Mountain Fynbos on clay rich soils (Boucher 1983). The acceptable inclusion of Coastal Rhenosterbosveld in the Fynbos Biome does not accord with the submission that Mountain Rhenosterbosveld is physiognomically and floristically similar to Coastal Rhenosterbosveld and 'occurs in the same geographic area' (Moll & Jarman 1984a). However, as

TABLE 4.—Acocks's veld types classified according to biomes

Savanna Biome	Grassland Biome	Nama-Karoo Biome	Fynbos Biome	Succulent Karoo Biome	Forest Biome
Coastal tropical forest types	Coastal tropical forest types	Tropical bush & savanna types	Coastal tropical forest types	Karoo & Karroid types	Coastal tropical forest types
1	3*	16	4*	26*	4*
2	5	17*	Karoo & Karroid types	28*	
3*	Inland tropical forest types	Karoo & Karroid types		31*	
6	tropical forest types			33*	
7				34*	
Inland tropical forest types	8*	types	False	False	
	False	24	Karoo types	Karoo types	
	bushveld types	26*			
8*	22	27		39*	
9	Temperate & transitional forest & scrub types	28*	Temperate & transitional forest & scrub types	43*	
Tropical bush & savanna types		29			
10		30			
11		31*			
12	Pure grassveld types	31*			
13		32*			
14		46			
15		47			
16*		48			
16*		49			
17*		50			
18		51			
19		52			
20		53			
False bushveld types		54			
21		55			
Karoo & Karroid types		56			
22		57			
23		43*			
25		58*			
32*		59	Pure grassveld types		
False Karoo types		60			
37*		61			
40*		62			
False grassveld types		63			
67		64			
68		65			
False sclerophyllous bush types		66			
70*					

\* Veld types present in more than one biome

mentioned above, the present study does indicate a very limited area within the Coastal Rhenosterbosveld zone which corresponds to Mountain Rhenosterbosveld. In their treatment of the all-embracing unit of 'Rhenosterbosveld', Moll *et al.* (1984) omit (and mask on the accompanying map, Moll & Bossi 1983) much of the areas of the Mountain Rhenosterbosveld of the interior escarpment owing to unavailable satellite imagery (Moll & Bossi 1984).

The border between Succulent Karoo and Nama-Karoo Biomes involves the greatest number of divisions (six) of Veld Types between two biomes, which possibly indicates the degree of past non-recognition of the Succulent Karoo Biome. Apart from Mountain Rhenosterbosveld that has just been discussed, a major division of Karroid Broken Veld was found to be necessary. Although

Acocks (1975) considers this Veld Type as a single unit, he clearly recognizes a division into Great Karoo, where grasses are 'surprisingly numerous', and Little Karoo, including the Robertson Karoo, where succulents are dominant and grasses are scarce. However, the vegetation of the south-western part of the Great Karoo (Laingsburg District) was found to satisfy the criteria for the Succulent Karoo Biome. The demarcation between Succulent Karoo and Nama-Karoo Biomes in the Karroid Broken Veld therefore agrees with Acocks's (1975) subdivision of this Veld Type, but is modified in the Great Karoo. It is possible that the Succulent Karoo Biome extends further east, north of the Swartberg but is unmappable. The Western Mountain Karoo is fairly evenly divided between the Succulent Karoo and Nama-Karoo Biomes. This division corresponds well with Acocks's (1975)

TABLE 5.—Veld types occurring in two or more biomes with a shortest cross distance of 20 km in each biome and showing the basis for the division of the veld types

Veld type number	Biomes	Basis for division
Acocks (1975)		
3	Grassland, Savanna	Altitude, literature <sup>1</sup> , pers. comms <sup>2</sup>
4	Forest, Fynbos	Relief, pers. obs <sup>3</sup> , detailed map by C. Geldenhuys <sup>4</sup>
8	Grassland, Savanna	Altitude, latitude, pers. comms, pers. obs
16	Nama-Karoo, Savanna	Rainfall <sup>5</sup> , literature, pers. comms, pers. obs
17	Nama-Karoo, Savanna	Rainfall, literature, pers. obs
26	Nama-Karoo, Succulent Karoo	Literature, pers. comms, pers. obs
28	Nama-Karoo, Succulent Karoo	Literature, pers. comms, pers. obs
31	Nama-Karoo, Succulent Karoo	Literature, pers. comms
32	Nama-Karoo, Savanna	Rainfall, pers. obs
33	Nama-Karoo, Succulent Karoo	Literature, pers. comms, pers. obs
34	Fynbos, Succulent Karoo	Literature
37	Savanna, Nama-Karoo	Literature, pers. comms, pers. obs
39	Nama-Karoo, Succulent Karoo	Pers. comms, pers. obs
40	Nama-Karoo, Savanna	Rainfall, pers. comms, pers. obs
43	Nama-Karoo, Succulent Karoo, Fynbos	Proximity primarily to Fynbos; Nama-Karoo and Succulent Karoo, mapping expediency
58	Nama-Karoo, Grassland	Altitude, literature, pers. comms
70	Fynbos, Savanna	Literature, pers. comms, pers. obs
Giess (1971)		
2	Desert, Nama-Karoo	Rainfall, pers. comms
3	Desert, Nama-Karoo	Rainfall, pers. obs
39	Desert, Nama-Karoo, Succulent Karoo	Rainfall, pers. comms, pers. obs
4	Nama-Karoo, Savanna	Latitude, rainfall, literature, pers. obs
8	Nama-Karoo, Savanna	Altitude, rainfall, pers. obs
9	Nama-Karoo, Savanna	Rainfall, pers. obs
13	Nama-Karoo, Savanna	Rainfall, literature, pers. comms

<sup>1</sup> Literature includes maps, annotated photographs, published and unpublished reports and literature consulted but not cited

<sup>2</sup> Pers. comms are consultations with those cited in the acknowledgements

<sup>3</sup> Pers. obs are the personal observations of the authors

<sup>4</sup> Unpublished map

<sup>5</sup> Rainfall refers to mean annual rainfall

division of this Veld Type into a semi-succulent form (Succulent Karoo Biome) and into an almost non-succulent form associated with grasses (Nama-Karoo Biome). The majority of Acocks's (1975) Succulent Karoo (Veld Type 31) falls within the Succulent Karoo Biome. The Steytlerville Karoo has been excluded from the Succulent Karoo Biome and is climatically distinct from the remainder of Veld Type 31. Acocks (1975) himself seems to doubt the affinities of the Steytlerville Karoo with his Succulent Karoo Veld Type and indicates its affinity to parts of the Nama-Karoo area. Acocks's (1975) False Succulent Karoo Veld Type is excluded from the Succulent Karoo Biome with the minor exception of two small outliers around Calvinia and in Namaqualand. The border between the Succulent Karoo and Nama-Karoo Biomes in the vicinity of the largest area of False Succulent Karoo is approximate due to inadequate vegetation data and absence of climatic stations. Acocks (1975) indicates the unsuitability of this area for Succulent Karoo, also in terms of rainfall seasonality, and available evidence suggests that this marginal area falls within the Nama-Karoo Biome (A. le Roux pers. comm.; O.H. Volk pers. comm.). The eastern outliers of False Succulent Karoo are unquestionably part of the Nama-Karoo Biome. The Namaqualand Broken Veld of Acocks (1953) extends from Namaqua-

land up the Orange River Valley to Kakamas and thus extends the Succulent Karoo Biome to deep into the Nama-Karoo Biome. However, in 1975, he (Acocks 1975 — Addendum) limits the extent of this Veld Type up the Orange River Valley to Vioolsdrift, which accords (with the exception of the extension of the Succulent Karoo Biome for a short distance up the Orange River Valley) with the division between the Succulent Karoo and Nama-Karoo Biomes. In South West Africa/Namibia, the Succulent Karoo Biome corresponds with Giess's (1971) 'Desert and Succulent Steppe (Winter rainfall area)' but the border between the Succulent Karoo and Nama-Karoo Biomes lies farther west. The transitional nature of the border area between the Succulent Karoo and Desert Biomes has been indicated above.

The border between the Nama-Karoo and Desert Biomes agrees closely with Giess's (1971) border between 'Semi-desert and Savanna Transition (Escarpmment zone)' and the Central and Southern Namib. The association of the border with arid grasslands has been discussed above. The border between the Nama-Karoo and Savanna Biomes in South West Africa/Namibia is associated with the escarpment zone which includes some southward-extending outliers of the Savanna Biome. Farther inland, the border intersects the parallel dune area of the southern Kalahari [Giess's 1971, Mixed

Tree and Shrub Savanna (Southern Kalahari)] as discussed, in terms of biome interface areas, above. In the northern Cape Province, the southern Kalahari is included in Acocks's (1975) Kalahari Thornveld (Veld Type 16) which is similarly intersected. This Veld Type is divided southwards, which is not unexpected, since this is a very broad Veld Type and is one of Acocks's (1975) most undersampled areas. The invasion of savanna areas by elements of Nama-Karoo (Acocks 1975, 'Kalahari Thornveld invaded by Karoo', Veld Type 17) appeared to be uneven and only small parts of this Veld Type were consistent with the Nama-Karoo Biome. In contrast, the northern extremities of Form c of the Orange River Broken Veld (Acocks 1975) do not comply with Nama-Karoo Biome criteria but with those of the Savanna Biome and are mapped accordingly. The False Orange River Broken Veld (Veld Type 40 of Acocks 1975) is, for similar reasons, divided almost equally between the Nama-Karoo and Savanna Biomes.

In the eastern Cape Province, those parts of the Savanna Biome bordering on the Nama-Karoo Biome deserve special attention. The savanna Veld Types concerned are Spekboomveld and the Fish River Scrub form, together with the Addo Bush and Sundays River Scrub subforms of the Valley Bushveld. These two Veld Types in this area are easily interpreted in different ways. In certain parts of these areas, the codominance of phanerophytes and chamaephytes (Archibald 1955) suggests the existence of a biome different to the seven biomes recognized in southern Africa and corresponds to the 'missing biome'. As with Mountain Rhenosterbosveld mentioned before, these marginal communities of today may be tomorrow's new biome (Heydorn & Tinley 1980 quoted Lubke *et al.* 1984) in the theoretical relationships of life forms in Fig. 8. Succulent low phanerophytes are dominant in some other areas which may be interpreted as 'low succulent forest'. Acocks (1975) states that Addo Bush is related to Alexandria Forest which, as discussed above, is a marginal type. In many of the borders in this region it has been shown that 'pseudo-fynbos' exists with codominance of phanerophytes, chamaephytes and hemicryptophytes. These unusual units form a patchy mosaic superimposed on a matrix of savanna. Valley Bushveld and Spekboomveld are subtropical thickets relating to those in the equatorial and tropical regions of Africa and are not of the Karoo or Karroid type (Heydorn & Tinley 1980). Addo Bush is reminiscent of thickets of the Arid Lowveld (Veld Type 11 of Acocks 1975) in the Transvaal and northern Natal (Acocks 1975). Although these areas of the eastern Cape Province have various life form combinations, phanerophytic dominance remains constant but, on average, is repetitiously associated with hemicryptophytic co-dominance which results in savanna.

Another Veld Type with dominant succulent plants in close proximity to Spekboomveld and Valley Bushveld in the eastern Cape Province, is Noorsveld (Veld Type 24 of Acocks 1975). Despite some affinities with parts of Valley Bushveld, variation in height near the

phanerophytic-chamaephytic limit of the dominant species, *Euphorbia coerulescens* Haw. and insufficient data, makes life form categorization difficult at biome scale. This Veld Type was included in the Nama-Karoo Biome, primarily on the basis of climatic relations (Fig. 10). The dominant succulents in many areas of the eastern Cape Province differ in several respects, notably in size, from those in areas with greater concentration of winter rainfall in the Succulent Karoo Biome. This difference is also evident in terms of photosynthetic pathways where the majority of plants from part of the winter rainfall area are CAM, whereas in part of the eastern Cape Province, most succulents are intermediate between CAM and C<sub>3</sub>-type photosynthesis (Mooney *et al.* 1977).

The border between Nama-Karoo and Grassland Biomes in the eastern Cape Province, excludes all of the Karroid *Merxmuellera* Mountain Veld (Veld Type 60 of Acocks 1975) from the Nama-Karoo Biome. This Veld Type contains the most arid parts of the main body of the Grassland Biome and is, therefore, the most marginal grassland type within this body. At higher altitudes within this Veld Type, grassland is best developed although some phanerophytes can occur locally. At lower altitudes, more mixing with chamaephytes is found (Van der Walt 1980). Data for redefining Acocks's (1975) border of this Veld Type were insufficient. The part of the Grassland Biome that has been invaded by karroid elements is included in the Nama-Karoo Biome, and corresponds to part of the False Upper Karoo (Veld Type 36 of Acocks 1975). There is some uncertainty regarding the position of the south-western limits of the original grassland in this Veld Type.

Acocks (1953) suggests that this south-western limit lay roughly between Murrarysburg and Petrusville. Later, Acocks (quoted Werger 1973) suggested that False Upper Karoo may be divided into a southern and a northern part with the Orange River as boundary. On the basis of the division between the Nama-Karoo and Grassland Biomes in the moisture matrix (Fig. 10) this limit was mapped (Fig. 15) and was found to approximate Acocks's (1953) limit and not the latter quoted division. The *Themeda-Festuca* Alpine Veld (Veld Type 58 of Acocks 1975) is a large unit covering most of the high altitude area of the Grassland Biome but also contains the entire outlier of the Nama-Karoo Biome (see above). Invasion of Grassland by Thorn (Veld Type 22 of Acocks 1975) is mapped as part of the Grassland Biome, although indeterminable large areas are savanna. The Pondoland Coastal Plateau Sourveld (Veld Type 3 of Acocks 1975) was divided into Grassland on the Plateaux and Savanna (with unmappable forest patches) in the lower lying areas.

Although much of the moist grasslands of Natal have sometimes been regarded as Forest, climatic evidence does not adequately support this notion. Palaeoecological evidence suggests that the moist grasslands of Natal have been dominant features of the landscape from the Holocene at least (Huntley 1984). Remains of

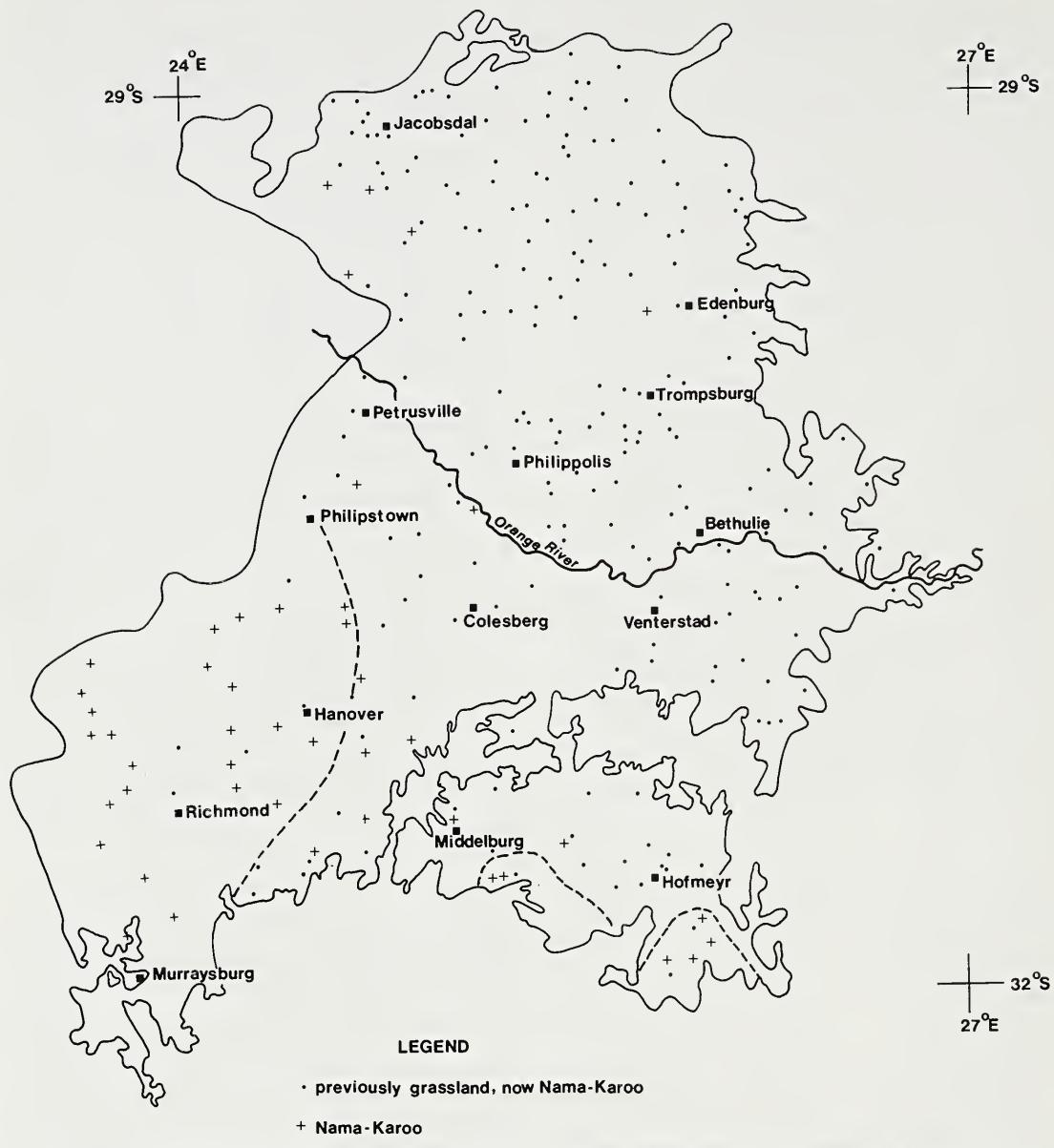


FIG. 15.—The False Upper Karoo (Veld Type 36 of Acocks, 1975) which contains 'the most spectacular of all changes in the vegetation of South Africa' (Acocks, 1975) in the form of invasion of grassland by elements of the Nama-Karoo Biome. The approximate border between original Grassland and Nama-Karoo Biomes is indicated by broken lines and is determined on the basis of the division between these two biomes in the moisture matrix (Fig. 10). Each symbol represents a weather station.

grassland animals have been found in deposits as old as 8 000 years BP (Mentis & Huntley 1982; Tainton & Mentis 1984) and it is 'difficult to conceive that forest was ever continuous' (Mentis & Huntley 1982). On the slopes below the main escarpment in Natal, Killick (1978a) postulates that ever since the climate included a dry season with natural fire, grassland and not forest has been the predominating community. Also in the southern Cape, the present drier climate does not favour forests which must be considered relics of a much wetter climatic period (Van Daalen 1981). The North-Eastern

Mountain Sourveld (Veld Type 8 of Acocks 1975) is divided between the Grassland Biome at higher altitudes and the Savanna Biome at lower altitude. This boundary was found to increase with altitude as latitude decreased northwards which is related to temperature limits for grassland (Fig. 12). This is consistent with the absence of grassland from this Veld Type at biome scale north of the Tropic of Capricorn. Although Bankenveld (Veld Type 61 of Acocks 1975) has sometimes been considered as potential savanna (for example, Acocks 1975) this is not supported by climatic evidence (Fig. 12; Appendix

2) and in many areas temperature minima are extreme. Use of the Faunal Resemblance Factor indicates a far greater similarity between Bankenveld and Acocks's (1975) pure grassveld types than between Bankenveld and bushveld types of the Transvaal (Rautenbach 1978b).

### 3.5 Concluding remarks

It is evident that the Summer Aridity Index together with rainfall seasonality successfully differentiates most of the biomes of southern Africa. The relationship between chamaephytic and hemicryptophytic dominance is particularly dependent on rainfall seasonality at higher SAI values. In the summer and strong summer rainfall areas, these two life forms are codominant, whereas in the winter and strong winter rainfall areas they are not both codominant. The success of the Summer Aridity Index can mainly be accounted for by the inclusion of both moisture and temperature, adequate levels of which are required for optimum plant growth. The index allows for low growth rates of plants in winter despite an adequate moisture supply, such as reported for Namaqua-land (Van Rooyen *et al.* 1979). The emphasis on precipitation, seasonality and temperature in this study has

recently been successfully used to differentiate major vegetation units of North America (Sowell 1985). After systematic consideration of 24 climatic variables, he found strongest correlation with the three climatic parameters used in this study.

In terms of both dominant life forms and differentiating climatic factors, biomes of southern Africa are not equally different (Fig. 16). Greatest differences exist between the Grassland and Succulent Karoo Biomes and least differences between the Forest and Savanna Biomes. For example, in the latter combination, only hemicryptophytic codominance has to be removed or added to result in forest or savanna respectively. The Succulent Karoo Biome generally has more differentiating features than the other biomes which fully justifies its biome status.

The basic spatial relationships of the biomes of southern Africa are summarized schematically in Fig. 17, where the depicted biome areas are proportional to actual areas and where all biome interface types are indicated. The Nama-Karoo Biome interfaces with the greatest number of other biomes and the Grassland Biome interfaces with least other biomes. The area with greatest concentration of different biome interfaces (Fig. 17) corresponds to the southern and eastern

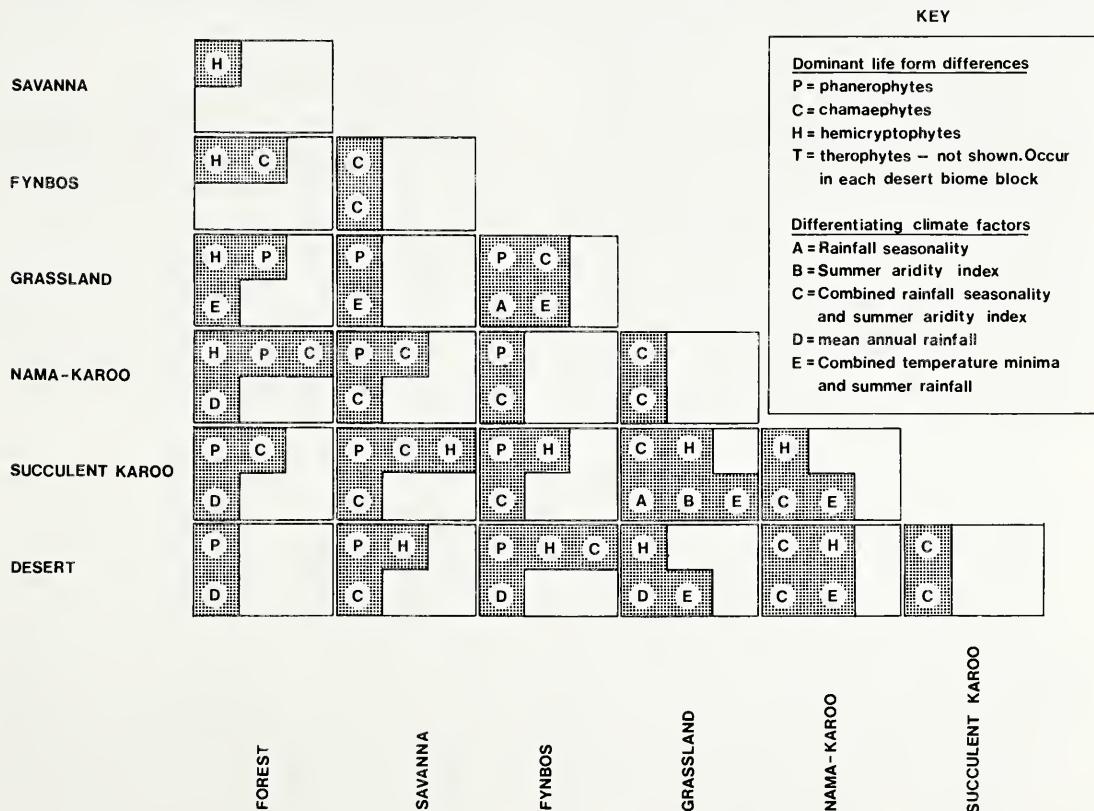


FIG. 16.—Synopsis of main life form and climatic differences between biomes. The dominant life form differences appear in the upper half of each matrix cell, and differentiating climatic factors (based on Figs 10 & 12) appear in the lower half. Climate factor C was not considered independent of A and/or B. Climate factor D was usually not independent of C. Where one factor was dependent on another listed, only one of these is listed per cell.

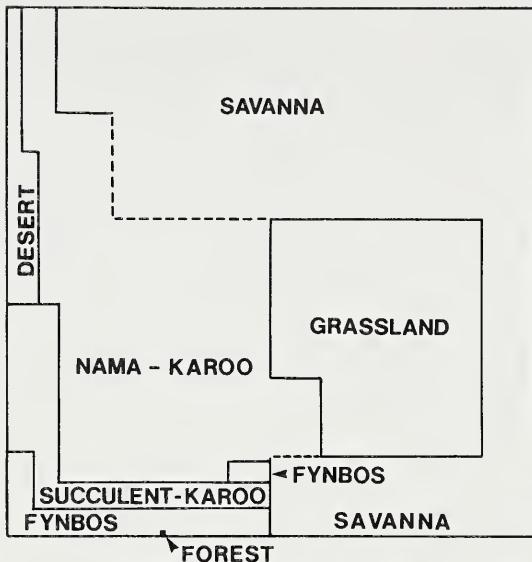


FIG. 17.—Schematic representation of the biomes of southern Africa with depicted biome areas proportional to actual areas and indicating all biome interface types. The dotted line indicates where 'Pseudofynbos' can occur in interface areas.

regions of the Cape Province. The vegetation of the eastern Cape Province is particularly heterogeneous and potentially confusing, owing to, for example: presence of 'pseudo-fynbos' at the Nama-Karoo and Savanna Biomes interface; various interpretations of Spekboomveld and Valley Bushveld; Alexandria Forest anomalies; intermediate biome status of Noorsveld; preponderance of phanerophytic succulents in many areas; presence of fynbos elements with savanna structure; presence of the most arid and marginal part of the Grassland Biome with mixing of other life forms; and invasion of parts of grassland by savanna elements. In addition, the border between Valley Bushveld and forest patches is sometimes decidedly indeterminate. In different context, the region as a whole has been described as a huge tension zone where four major phytochoria converge (Cowling 1983).

This confusion in the biome relations in the eastern Cape Province has led to Acocks (1975) being criticized by a number of authors, notably those working in the eastern Cape Province, for the way he grouped unrelated types into a single Veld Type and his classification above the level of Veld Types (Lubke *et al.* 1984). Although the latter criticism is undisputed, the majority of mapped borders of Acocks's (1975) Veld Types in South Africa coincide with biome borders. By contrast, in South West Africa/Namibia, the majority of borders between Giess's (1971) vegetation types did not correspond as closely with biome borders.

Succulence is not limited to the Succulent Karoo Biome with its preponderance of chamaephytic succulents and there are some direct transitions to phanerophytic succulents of parts of the Savanna Biome in the Little Karoo. Similarly, there is a direct transition of dominant succulents from the Noorsveld of the Nama-Karoo Biome to the Spekboomveld of the Savanna Biome in the eastern Cape Province. Areas with dominant succulents also occur elsewhere in the Nama-Karoo and Savanna Biomes, but not at biome scale, for example, in the lower Orange River Valley and parts of Sekukuneland in the Transvaal. Succulence is generally associated with areas of lower rainfall and less extreme temperature minima in each of the respective biomes. In a broader context, succulence is given by:

$$\text{succulence} = f(R, T_{\min}, T_{\max}, U)$$

where  $R$  is rainfall,  $T_{\min}$  is temperature minima,  $T_{\max}$  is temperature maxima and  $U$  is utilization level. Succulence is usually maximized where  $R$  is low,  $T_{\min}$ ,  $T_{\max}$  and  $U$  are high.

Although forest patches are limited to areas of higher rainfall, gallery forest can exist with the aid of subterranean water in any of the biomes, including desert zones. Despite the easily recognizable and obvious physiognomy of gallery forests, they, like other minor intrusive biological features remain unmappable at biome scale.

## 4 Description of the biomes

### 4.1 Overview

To avoid a plethora of incompatible soil units, the unified broad soil classificatory scheme of MacVicar (1973) was used for the Republic of South Africa. For other areas, the best available local information was used. Although the soil map for southern Africa of Harmse (1978) covers the entire study area, it emphasizes the diversity of soils within units, so that the comparability of units on a biome scale is rendered impracticable. MacVicar's (1973) soil map for South Africa, which forms the basis for the South African part of Harmse's (1978) map, emphasizes a broader approach. Geological units of each biome were determined using various small scale sources that follow the recommendations of the South African Committee for Stratigraphy (SACS) (1980). This resulted in a comparable number of units used for soils and geology.

Climatic descriptions within each biome are usually limited to moisture, temperature and seasonality for which data are more readily available. Many other climatic parameters, such as relative variability of annual rainfall, are less relevant in their effect on dominant life form combinations and are not discussed.

Plant production estimates are limited to above-ground dry matter production (including stubble) of natural vegetation and apply to broad areas within the biome and not to local extremes. Plant biomass is taken as equivalent to standing crop and is also expressed in terms of above-ground dry matter over broad areas. Where hemicryptophytes are dominant, total plant biomass is, unlike production, often highly variable and depends on local utilization practices. Although the photosynthetic pathways of C<sub>3</sub>, C<sub>4</sub> and CAM of some plant groups are associated with certain biomes, there is little correlation between these photosynthetic pathways and the mean annual dry matter production under field conditions. Osmond *et al.* (1982) found no difference between productivity of C<sub>3</sub> and C<sub>4</sub> plants, irrespective of rainfall.

Soils may serve as a basis for subdivision of certain biomes, but because soils usually vary greatly over short distances, such subdivision can rather be expressed in terms of climatic criteria. These are fundamental deter-

mining factors in pedogenesis which can also be better expressed at smaller scales. Therefore, Huntley's (1984) subdivision of the Savanna Biome primarily on the basis of moisture is preferable to sole reliance on soil characteristics. Even in desert, in most cases the development of communities is an indirect response to soils and a direct response to water availability in the soils (Robinson 1976).

Space limitations have precluded excessive detail in the descriptions of the biomes. The descriptions emphasize salient features of each biome which are presented in a consistent order to facilitate comparison.

### 4.2 Desert Biome

The term desert (Table 6) is long established and is derived from the Latin word for wastes or abandoned or forsaken places. The Desert Biome in southern Africa corresponds to what is known as the Namib Desert (Giess 1971; Moritz 1970) which forms a broad coastal belt north of the Lüderitz area in South West Africa/Namibia. The area of this biome south of 22° S is approximately 53 000 square kilometres (Table 3). The topography of the gently sloping coastal plain, which is usually below 1 000 m above mean sea level, is broken by a sea of sand dunes up to 300 m high in the south and by some inselbergs, mainly in the north. The main geological units are Quaternary and Tertiary deposits followed by the Swakop Group of the Damara Supergroup. Other units include Salem Granite and older Basement Complexes. In the usually dry drainage systems, which by definition, do not form part of this biome, flow is from east to west. The major rivers are the Swakop which with rare floods of sufficient magnitude can reach the Atlantic Ocean and the Kuiseb in which surface flow no longer reaches the ocean. Other rivers to the south end abruptly in the inland sand dunes. The main soil units found in the Desert Biome (Robinson 1976) are: 1, undifferentiated dune sand with sand grains frequently cemented by limestone or gypsum in the interdune valleys; 2, limestone soils derived from calcrete occurring over large areas of the plains; 3, gypsum soils of the fog zone. The silts, watercourse gravel and saline soils are generally associated with drainage lines and are not defined as desert. Water

is far less important than wind as an erosion agent in this desert. Sand dune dynamics are governed primarily by wind. The resultant mobile dunes prevent plant establishment and may smother any established plant cover. The advancement of dunes with the prevailing southerly summer winds is halted by episodic floods of sufficient frequency in the Kuiseb River and the plains north of the river tend to be without sand dunes except near the coast.

conspicuous perennial plants of the mobile dunes (*Stipagrostis sabulicola* (Pilg.) De Winter and *Trianthema hereroensis* Schinz) have an extremely low cover which can be greatly exceeded by that of the therophytes of the interdune areas (see Robinson 1976). In the central Namib Desert, all the grasses and some sedges are of the C<sub>4</sub> type, whereas the majority of the other species are C<sub>3</sub> with some CAM plants (Vogel & Seely 1977). Along the coast north of the Swakop River, a narrow belt of

TABLE 6.—Biome nomenclature showing terms for the proposed biomes, equivalent traditional terms in southern Africa, descriptions based on dominant growth forms derived from Edwards (1983), and dominant life forms

Proposed Biome (and Afrikaans term)	Traditional term in southern Africa	Description	Dominant life forms
Desert (Woestyn)	Desert	(Therophytic) desert	Therophytes
Grassland (Grasveld)	Grassland	Grassland	Hemicryptophytes
Succulent Karoo (Sukkulente Karoo)	Karoo	Dwarf shrubland	Chamaephytes
Forest (Woud)	Forest	Shrub/woodland	Phanerophytes
Nama-Karoo (Nama-Karoo)	Karoo	Grassy, dwarf shrubland	Hemicryptophytes chamaephytes
Savanna (Bosveld)	Savanna	Grassy, shrub woodland	Hemicryptophytes phanerophytes
Fynbos (Fynbos)	Fynbos	Grassy, dwarf shrubby, shrub/woodland	Phanerophytes, chamaephytes, hemicryptophytes

The climate is characterized by summer and strong summer rainfall, greatest summer aridity, and mean annual rainfall from approximately 13 mm in the west to 70 mm (or 85 mm in places) on the inland margin (see Section 3.2). The extreme aridity is attributed, in part, to most of the rain originating over the distant Indian Ocean and to the cold Benguela current which, together with the hot land mass, is also instrumental in forming coastal fog. Daily frequency of fog exceeds 50% per annum and, although mainly limited to the coastal belt, occasionally extends farther inland with a frequency decreasing to about 10% halfway to the inland margin of the biome (Robinson 1976). The biome has the greatest range in average annual duration of bright sunshine, namely, from less than 50% to greater than 80% of that possible (Schulze, B.R. 1965). The mean lowest minimum temperature for the coldest month, in contrast to the other biomes, does not generally drop below 0°C. The length of the period in which frost can occur is generally less than 30 days per annum (Schulze, B.R. 1965). The average number of days with thunder is generally less than 5 per year, which is low compared to that in other biomes.

The vegetation of the Desert Biome is characterized by dominance of therophytes. Water stress in plants of the Desert Biome is, therefore, overcome primarily by drought evasion in the form of seed. The vegetation of drainage lines, including flood plains, does not form part of the Desert Biome (see Section 2.2). Therophytes are usually graminoid and cover can vary temporally or spatially from zero to closed canopy (Edwards 1983) depending on rainfall distribution and amount. Toward the inland margin of the biome, exceptionally good rains can result in switching of certain plants from therophytes to relatively short-lived hemicryptophytes. The

vegetation, usually less than 200 m wide, occurs. This vegetation consists of dwarf shrubs which form small hummock dunes. The well-known chamaephyte *Welwitschia mirabilis* Hook. f. of the 'Namib Desert' is not part of the defined Desert Biome because it is mainly limited to the run-in areas of broad drainage lines or washes (Kers 1967). The plants with their deep tap roots are, therefore, not directly dependent on rainfall and cannot qualify as part of a rain desert (Zohary 1973). Plant species diversity in the Desert Biome is lower than that in any other biome. Some plants are adapted to make use of water from fog. Although generally inadequate for germination of seed, fog water can be an important supplementary source of water for the survival of some of the rare perennials. It has been established that the dune plant *Trianthema hereroensis*, which is restricted to the western half of the dune sea with greater frequency of fog, imbibes fog through its leaves. This is essential for the water balance of this species (Louw & Seely 1980). The dune plant *Stipagrostis sabulicola* has a very extensive shallow root system (extending as far as 20 m from the main plant) which, apart from presumably helping to anchor the plant, has been shown to be capable of absorbing fog condensed on the ground (Louw & Seely 1980). This species extends farther east where rain increasingly replaces fog as source of precipitation. The desert environment, almost exclusively, does not permit succession of one plant community to another where most plants are short-lived. Mean annual above-ground plant production (outside run-in areas) depends primarily on mean annual precipitation and ranges from about 50 to 350 kg ha<sup>-1</sup>a<sup>-1</sup> (derived, Rutherford 1980) at biome scale. This material is not usually accumulated from year to year and is, therefore, altogether inadequate for carrying fire.

The fauna of the Desert Biome is unusual and has attracted much interest. It has an abundant insect fauna (Seely 1979) but also some impoverished groups such as the malacofauna (Van Bruggen 1978). Many animal species, for example, those of Lepidoptera (Pinhey 1978) and some larger mammals, depend on water course vegetation and are not resident in the therophytic desert. Some other animals, for example, larks (Alaudidae), which are normally resident outside the biome, enter after rain has fallen in the Desert Biome (Willoughby, quoted Seely 1979). Organic detritus, consisting of grass remnants and animal remains, may be imported into dune valleys by wind and is a food source for other animals (Walter 1979). Some tenebrionid beetles can utilize fog water (Seely 1979) and fog allows activity of certain snails (Van Bruggen 1978). In Namib beetles, the upper lethal limits of temperature are markedly higher than for non-desert species (Edney, quoted Seely 1979), a phenomenon termed 'maxithermy' (Hamilton, quoted Seely 1979). Many birds have a high tolerance to hyperthermia and are able to utilize saline waters (Maclean 1974). Most of the specialized reptiles inhabiting the desert are lizards. Reptiles of importance include the extensively webbed foot gecko (*Palmatogecko rangei*) of the dunes, the widespread barking gecko (*Ptenopus garulus maculatus*) and the typical dune snake, Peringuey's adder (*Bitis peringueyi*) (Poynton & Broadley 1978).

The conservation status of the Desert Biome is exceptionally good. Most of the area is conserved by the major portion of the Namib-Naukluft Park as well as by much of the unworked restricted diamond areas.

The suggested subdivision of biomes is on the basis of water availability (see Section 4.1). The desert can thus be divided into three zones which parallel the coast. These are the narrow coastal zone with frequent fog and mean annual rainfall of about 13 to 20 mm; a central zone in which fog is less frequent and mean annual rainfall is from about 21 to 50 mm; and an inland zone with little fog and mean annual rainfall from about 51 to 70 mm, or to 85 mm in places. These zones generally correspond with Besler's (quoted McClain 1984) climatic zones for this area. The coastal fog zone is cooler with evaporation almost half of that in the other two zones. Maximum temperature in the central zone is slightly higher than in the inland zone and possibly reflects the combination of lower rainfall and less frequent fog.

A major impetus in research of the Desert Biome was effected by the establishment of a desert research station at Gobabeb in 1962 which attracts large numbers of researchers from many parts of the world, and the later expansion of this station and proclamation of a large conserved area by the South West African Administration.

Direct utilization of the biota is negligible due to low potential productivity and low carrying capacity. Urbanization is limited to areas on the coast, notably at Walvis Bay and Swakopmund. The unique landscape lends itself to tourism which is being promoted in the above-mentioned park. The main economic resources of the Desert Biome are its mineral wealth which includes

diamonds, uranium, lead, copper, gold and silver. Indigenous human inhabitants are the few Topnaar Hottentots who live along some main water courses that traverse the desert.

#### 4.3 Forest Biome

The term forest is derived from the old French with a relatively wide meaning which has been narrowed in South Africa to pertain to woody vegetation with continuous canopy cover. Although the only forest area of biome dimension occurs in the southern Cape Province, many smaller forest patches are distributed in higher rainfall areas from the Fynbos Biome along the eastern escarpment and eastern seaboard in both Grassland and Savanna Biomes. Forest can occur from sea level to 2 134 m above mean sea level at Nelson's Kop in the Grassland Biome (Cooper 1982). The Forest Biome is by far the smallest in southern Africa (see Section 3.4). The Forest Biome and forest patches can occur on a wide variety of terrain types but in areas other than coastal flats, they usually occur in relatively specialized habitats such as landscape incision breaks. The main geological unit of the mapped unit is the Table Mountain Group of the Cape Supergroup. The soils are usually well drained and occur on virtually all soil types (Van Daalen 1981). Soil erosion is usually negligible (except in some clear-cut areas) due to the high protective plant cover. Forest or forest patches are limited to areas with mean annual rainfall greater than 525 mm with strong winter rainfall and greater than 725 mm with strong summer rainfall. Humidity is high because of plant transpiration and poor air circulation (Smith 1974). Frost does not occur (Adamson 1938). Lightning flash density for forest and forest patches varies widely from less than one to greater than eight flashes per square kilometre per year (Edwards 1984).

The vegetation of the Forest Biome is characterized by dominance of mostly evergreen (Tinley 1975) phanerophytes which are usually mesophanerophytes. Canopy cover is continuous, being overlapping or nearly so (Edwards 1983). The vegetation is multilayered with an open to closed understorey of phanerophytes, chamaephytes or hemicryptophytes. Therophytes are particularly rare. The forest structure results in reduced light levels in the subcanopy area where epiphytes, ferns and lianes can be common. Tallest phanerophytes are those of *Podocarpus falcatus* (Thunb.) R. Br. ex Mirb. which can exceed a height of 40 m. The forest patches are not floristically uniform and the coastal lowland forest patches north of Algoa Bay are differentiated from the afromontane forests along the Drakensberg escarpment and on the coastal plain of the southern Cape Province. In forest patches of the intermediate area there is considerable floristic mixing (Huntley 1984). These two floristic types have been identified as two separate phytoclimates which extend north of southern Africa (Werger 1978a). Available evidence suggests that there is little important structural difference between the two floristic types.

TABLE 7.—Areas conserved in each biome in the Republic of South Africa according to organizations responsible

Responsible organization	Areas* conserved in each biome						Totals for each organization							
	Savanna km <sup>2</sup>	% of biome	Fynbos km <sup>2</sup>	% of biome	Grassland km <sup>2</sup>	% of biome	Nama-Karoo km <sup>2</sup>	% of biome	Succulent Karoo km <sup>2</sup>	% of biome	Forest km <sup>2</sup>	% of biome	Total km <sup>2</sup>	% of total area
National Parks Board	29 162	7,13	49	0,07	89	0,03	403	0,12	12	3,88	29 715	2,43		
Dept of Environment Forestry	257	0,06	10 335	15,66	1 472	0,47			101	32,69	12 765	1,05		
S A Defence Force	1 846	0,46	164	0,23	388	0,12	1 242	0,36	251	0,31		3 891	0,32	
Natal Parks Board	1 536	0,38			831	0,26						2 367	0,19	
Transvaal — Province	1 038	0,25			380	0,12							1 418	0,12
Cape — Province	140	0,03	275	0,39	71	0,02	359	0,10	75	0,09		920	0,08	
Dept of Co-operation & Development	585	0,14			82	0,03						667	0,05	
O F S — Province	147	0,04			159	0,05	356	0,10				662	0,05	
Cape — subsidized private	52	0,01	241	0,34	48	0,02	74	0,02	61	0,07		476	0,04	
Totals for each biome	34 763	8,50	11 664	16,69	3 520	1,12	2 434	0,70	387	0,47	113	36,57**	52 881	4,33

\* Areas derived from NAKOR — National Plan for Nature Conservation: register of conserved areas — October 1984.

\*\* This total is for mapped forest only. For mapped forest and unmapped forest outliers the total % conserved is between 3,77 and 5,65.

Forests seldom burn, except under rare weather conditions, but fire can have marked effects on forest margins (Edwards 1984). Under extreme circumstances, ground fires have been observed to kill most forest trees, except those with deep roots, for example, *Ocotea bullata* (Burch.) Baill. (Kruger 1984). After ground fires pyric succession may be arrested at an early stage, with vegetation less than 2 m tall (Kruger 1984). This contrasts with four stages in the 'usual' successional sequence from establishment of forest initials to full establishment of canopy species. The full period of succession in forest is usually longer than that for any of the other biomes. In the absence of production measurements in the specific area, mean annual above-ground plant production is estimated, using other data, to range from 6 000 to 15 000 kg ha<sup>-1</sup> a<sup>-1</sup>. Above-ground biomass in the Forest Biome can exceed 235 metric tons per hectare.

Typical mammals include the bush pig (*Potamochoerus porcus*) and blue duiker (*Cephalophus monticola*). Twenty seven per cent of southern African mammal species occur in forest of which 12 species are endemic (Rautenbach 1978a). Bird abundance is correlated with structural complexity of the vegetation (Naveh & Whittaker 1979). Several bird species are typical of this biome and are often important in seed dispersal, and include the Knysna Loerie (*Tauraco corythaix*) and the Rameron Pigeon (*Columba arquatrix*). The majority of locally known land snails occur in forest where they are richly represented (Van Bruggen 1978). Relatively

few reptiles inhabit evergreen forests, and even these are most likely to be encountered at the forest edge or in clearings where the sun can penetrate (Poynton & Broadley 1978).

Only approximately 113 square kilometres of the Forest Biome is conserved (Table 7) which is smaller than minimum biome size (Table 8). Although this constitutes about 37% of the mapped Forest Biome, it constitutes a much lower percentage of the biome together with its unmappable outliers. A prominent alien plant invader in the Forest Biome is *Acacia melanoxylon* R. Br. (MacDonald & Jarman 1984).

Because the Forest Biome is barely of biome proportion and the range of variation within this area is limited, subdivision relative to that in the other biomes is inappropriate (see Section 6). Considerable research is being undertaken in the Forest Biome and its sub-biomic outliers. Most of this research forms part of the national indigenous forest research programme. The Directorate of Forestry of the Department of Environment Affairs is responsible for two thirds of the research projects. About 7% of published papers on fire research in south Africa concern forest (Scott 1984).

Indigenous timber production is the main form of direct utilization of resources in the Forest Biome and much sought-after and valuable timber types are black stinkwood (*Ocotea bullata*) and Outeniqua yellowwood (*Podocarpus falcatus*). In cleared areas, there are plantations of Slash Pine (*Pinus elliotti* Engelmann), Monterey

TABLE 8.—Conserved areas greater than the smallest mappable biome unit area (314 km<sup>2</sup>) in each biome in the RSA

Name of conserved area	Conserved areas* exceeding 314 km <sup>2</sup> in each biome					
	Savanna km <sup>2</sup>	Fynbos km <sup>2</sup>	Grassland km <sup>2</sup>	Nama-Karoo km <sup>2</sup>	Succulent Karoo km <sup>2</sup>	Forest km <sup>2</sup>
Kruger National Park	19 485					
Kalahari Gemsbok National Park	9 591					
P.W. Botha Training Area	1 080					
Umflozi Game Reserve	478					
Hawequas Mountain Catchment Area		1 159				
Koue Bokkeveld Mountain Catchment Area		963				
Matroosberg Mountain Catchment Area		950				
Groot Swartberg Mountain Catchment Area		919				
Groot Winterhoek Mountain Catchment Area		812				
Langebaan East Mountain Catchment Area		713				
Cederberg Wilderness Area		644				
Cederberg Mountain Catchment Area		620				
Hottentots Holland Mountain Catchment Area		604				
Langebaan West Mountain Catchment		588**				
Riviersonderend Mountain Catchment Area		582**				
Klein Swartberg Mountain Catchment Area		492**				
Kammanassie Mountain Catchment Area		475**				
Mkhomazi Wilderness Area			486**			
Giant's Castle Game Reserve			346**			
Riemvasmaak Training Area				702		
Schmidtsdrift Training Area				347**		
Total Area	30 634	9 521	832	1 049	0,0	0,0
% of biome	7,49	13,63	0,27	0,30	0,0	0,0
% of total area	3,44					

\* Areas derived from NAKOR — National Plan for Nature Conservation: register of conserved areas — October 1984.

\*\* May not meet the requirement for the shortest cross distance of a mappable unit.

Pine (*Pinus radiata* D. Don.), and Blackwood (*Acacia melanoxylon*). The grandeur of the forests (and their settings) enhanced by their rarity in southern Africa, makes them an important tourist attraction. Mineral exploitation in forest areas is usually very limited except on the dune forest outliers of northern Natal where titanium, zirconium, thorium and rare earths are exploited.

#### 4.4 Fynbos Biome

Fynbos is a vernacular term (literally meaning fine-leaved bush) long used to describe the vegetation of the Fynbos Biome. Already in 1916, Bews employed the term 'Fynbosch' in a scientific article and in 1927 Adamson proposed the same term as more suitable than 'Macchia' in South Africa. The term fynbos has recently gained acceptance by the international scientific community. The Fynbos Biome occurs in the south-western and southern Cape Province (see Section 3.4) and covers an area of about 70 000 km<sup>2</sup> (Table 3). The topography of the Fynbos Biome is dominated by the Cape Folded Mountain Belt bounded in the interior by Karoo basins and bounded by the coast to the south and west. Between the coast and mountains, the lowlands also form part of the biome. Maximum elevation above mean sea level is 2 325 m in the Klein Swartberg. The mountains include extensive areas with high rock cover pointing to the ruggedness of parts of the terrain.

The main geological unit is the Table Mountain Group followed by the Bokkeveld Group, both of the Cape Supergroup, Malmesbury Group of the Damara Supergroup and Quaternary and Tertiary deposits. Other units include Cretaceous deposits, the Witteberg Group of the Cape Supergroup and the Cape Granite Suite. The Mountain Fynbos is closely associated with the sandstones and quartzites of the Cape Supergroup.

The main perennial rivers of the biome are the Olifants and Berg which drain into the Atlantic Ocean and the Breede and Gouritz which drain into the Indian Ocean. On some of the mountain plateaux localized seasonal swamps occur.

The most common soil group in the Fynbos Biome, accounting for just under 50% of the area, is the undifferentiated rock and lithosol group mainly of the mountains. This is followed by weakly developed soils on rock. Other soil groups include sands, solonetzic soils, acid yellow-grey sand loams and podsols. The siliceous soils have a generally low nutrient status particularly on the mountains where soils can contain, for example, negligible amounts of extractable phosphorous (1–4 µg g<sup>-1</sup>) — see Kruger (1979b).

Erosion of soil on the mountains is usually limited. The longer term erosion of mountains is manifested as extensive slopes of bouldery debris and fans which in turn are subject to further erosion. In the area where the mountain chains change from east-west to north-south, major faulting is found and this area contains most of the epicentres of occasional earthquakes. On the coastal

forelands, the heavier soils are particularly erodable. The Fynbos Biome is limited to the strong winter, winter and even rainfall areas with mean annual rainfall ranging from about 210 mm to greater than 3 000 mm. During summer, mist precipitation from orographic cloud can occur on upper mountain areas, which may be particularly important to vegetation in the strong winter rainfall and winter rainfall areas. Short-lived snowfalls occur on the higher mountain peaks in winter. Fog is common along the west coast. Hail is rare. Winter frosts are rare on the coastal forelands but may be a common feature at higher altitudes (Adamson 1938; Kruger 1979b) but are not particularly severe (Fig. 12). The Fynbos Biome has incoming radiation of less than about  $120 \times 10^5 \text{ Jm}^{-2} \text{ day}^{-1}$  in winter which is lower than that in any other biome and which is approximately half that received by the strong summer rainfall areas in summer (Schulze & McGee 1978) where the combination of moisture and radiation provide for optimum plant growth. Summer wind, particularly in the south-western part of the biome, is often extremely strong, persisting for several days at a time and often deforms plants growing in exposed positions (Boucher 1978). Lightning flash densities are very low in most of the biome and flashes to ground may just exceed one flash km<sup>-2</sup> a<sup>-1</sup> in the east (Edwards 1984).

The Fynbos Biome is characterized by the codominance of usually evergreen, sclerophyllous phanerophytes, chamaephytes and hemicryptophytes, although at sub-biomic scale, variations in dominance occur. The vegetation can be literally described as open to closed grassy, dwarf shrubby, shrub/woodland (Edwards 1983) and generally does not exceed 3 m in height. In most of the biome, the hemicryptophyte component includes a low proportion of the Poaceae and a high proportion of the Restionaceae which have been considered diagnostic for the Fynbos Biome (Taylor 1978). The proportion of Poaceae increases east of 23°E. The basic three-layered Fynbos structure (Adamson 1938; Boucher 1978) is subject to age of the vegetation which affects the relative contribution of life forms (Van Wilgen 1981). Post-fire successional stages in fynbos have been described by Kruger & Bigalke (1984). In the immediate post-fire phase hemicryptophytes soon sprout, geophytes and therophytes flower, and some woody plants germinate. In the juvenile (regeneration) phase (up to 4–5 years), fynbos is quickly dominated by restioid plants and sprouting shrubs. Opportunistic shrubs mature and die but longer-lived phanerophytes begin to emerge from the canopy. In the transitional (maturing) phase (up to about 10 years) most plant species attain reproductive maturity. In the mature phase (up to 30 years), phanerophytes attain maximum height. Some chamaephytes begin to die and the cover of the herbaceous stratum is reduced. Few new plants establish. In the senescent phase (greater than 30 years) crown die-back of phanerophytes occurs and mortality accelerates. Codominance of phanerophytes, chamaephytes and hemicryptophytes is best developed in the transitional and early mature

phases. Larger phanerophytes are rare in fynbos, even in areas of high rainfall. Various reasons have been suggested to explain this lack and include high fire frequency (Moll *et al.* 1980), high wind intensity or lack of suitable mycorrhiza. There is a preponderance of grass species with C<sub>3</sub> photosynthetic pathways in the Fynbos Biome (Vogel *et al.* 1978). Phenological activity of the vegetation takes place through most of the year (Pierce 1984) and is, in many species, apparently out of phase with the annual march of climate (Kruger 1981), notably rainfall and temperature. Mountain fynbos is not limited to sandy soils but can also be found on some clay rich soils (Boucher 1983). The restriction of arid fynbos to Witteberg quartzites and the Karoo vegetation to Dwyka conglomerates along part of the inland margin of the Fynbos Biome has been explained primarily in terms of differences in soil water availability (Marloth, quoted Taylor 1978). *Elytropappus rhinocerotis* dominates large areas on heavy soils of the coastal forelands and parts of the interior (see Section 3.4). Although floristic affinities of the vegetation of these areas with fynbos on sandy substrates are low, it nevertheless is structurally similar (Van Rensburg 1962; Boucher & Moll 1981: see also Section 3.4).

The vegetation of the arid western part of the Fynbos Biome (southern Strandveld) is more spinescent and contains succulents. Other important variations (which are of limited extent) on the coastal forelands include fynbos on limestone and the dwarf fynbos of the Elim flats (Acocks 1975; Moll *et al.* 1984). Inland, a belt of arid fynbos flanks the more mesic fynbos of the mountains. Plant height usually decreases with altitude, although there is much variation, (Rutherford 1981) so that the vegetation on mountain tops tends to lack the larger life forms. In areas of poor drainage, particularly on some mountain plateaux, seasonal to perennial water-logging can occur and woody plants are usually excluded, as in dampbos in savanna.

The Fynbos Biome approximates the Cape Floristic Kingdom which, despite its minuscule size, has been recognized as one of the world's six floristic Kingdoms (Good 1964). Floristic diversity in the Fynbos Biome is high particularly at smaller mapping scales. Gamma diversity is apparently higher than in any of the world's biogeographic zones except perhaps the tropical rain forest, and the high delta diversities are apparently unmatched anywhere (Kruger & Taylor 1980). Many plant taxa are endemic to the Fynbos Biome. Seven plant families and about 210 genera and more than half the species are endemic to the biome (White 1983). Many species in the Fynbos Biome are rare, which may be correlated with the high delta diversity. This area contains 65% of the threatened and rare plants of the entire southern African Region (Hall *et al.* 1980). A relatively large number of species have showy inflorescences e.g. some species of *Protea*, *Leucospermum*, *Heliocrysum*, *Disa* and *Erica*.

Fire is a very important factor in the Fynbos Biome. Most fynbos is highly flammable due to the common

presence of combustible oils, finely divided canopies and continuous structure. The nature of fynbos fuels and the characteristic fire climate of strong frequent winds in the hot dry summer, combine to favour a fire regime unique in southern Africa (Kruger & Bigalke 1984). Fire frequency is variable but is not normally greater than once in four years due to insufficient fuel accumulation and the probability of fynbos escaping fire for more than about 25 years is low. Fires normally kill all above-ground parts of fynbos vegetation and usually consume most of the above-ground material except thicker stems. A large proportion of usually woody Fynbos plants are obligate seeders, that is, the whole plant (roots included) dies after fire and can only reproduce through seed. This largely distinguishes Fynbos from the other biomes in which fire is common. The period from germination to reproductive maturity (youth phase) varies greatly amongst species from 1 or 2 years to about 8 years. Where the frequency of fire is once or greater during the youth period of a species, any seed bank present will become depleted and the species is likely to become eliminated from the area concerned.

The reaction of fynbos vegetation to fire is summarized in terms of fire life forms in Fig. 18. The main conversions through fire of life forms to fire life forms are superimposed and highlighted on the theoretical

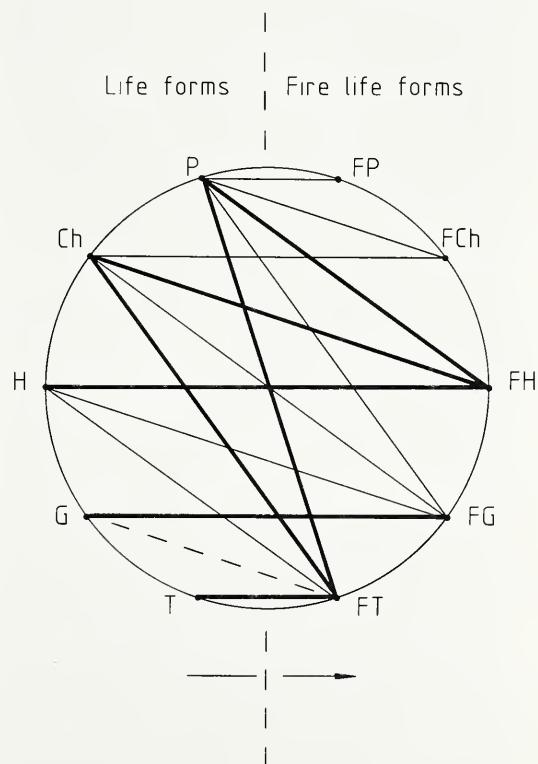


FIG. 18.—The relationship between life forms and subsequent fire life forms in the Fynbos Biome shown by bold lines. Abbreviations used are: P, phanerophyte; Ch, chamaephyte; H, hemicryptophyte; G, geophyte and T, therophyte.

possibilities given in Fig. 2. Both phanerophytes and chamaephytes become either reduced to ground level (fire hemicryptophyte) or to seed (fire therophyte) (compare with the savanna section 4.7). The former are sprouters and the latter are obligate seeders. Hemicryptophytes, geophytes and therophytes do not change their life form with fire. Parts of the Fynbos Biome have a high degree of summer aridity which can be as high as that of parts of the Desert Biome (Fig. 10). There are various morphological features of dominant plants in Fynbos that suggest adaptation to drought. These include aphyllly (e.g. in Restionaceae), cupressoid leaves (e.g. *Elytropappus rhinocerotis*) and ericoid leaves (e.g. in *Erica* and *Metalasia*). Above-ground plant production in fynbos has been based on long term biomass accumulation rates and the estimates of 1 000 to 4 000 kg ha<sup>-1</sup> a<sup>-1</sup> (Kruger 1977) are, therefore, necessarily underestimates and production can be expected to exceed 4 000 kg ha<sup>-1</sup> a<sup>-1</sup> in parts of the biome. Above-ground biomass (excluding dead plants) is dependent on the age of the vegetation and, although typically in the range of 6 to about 25 metric tonnes/ha (Rutherford 1978), can attain about 36 metric tonnes/ha<sup>-1</sup> (Van Wilgen 1981).

Various faunal elements are important in fynbos ecology. Many plant species are dependent for dispersal of their seed on ants (Bond & Slingsby 1983) and for pollination on birds (e.g. Cape Sugarbird — *Promerops cafer*) or on small mammals (Rourke & Wiens 1977). The greatest number of endemic animals in the Fynbos Biome is to be found amongst the invertebrates (Jarvis 1979). The area is rich in Lepidoptera, particularly the endemic, gramineous feeding Satyridae (Pinhey 1978). This biome is not very productive of food for mammals. The mammal fauna is small and most species are shared with adjacent biomes (Bigalke 1978). Only 18% of the mammal species of southern Africa occur in the biome of which 7 species are endemic (Rautenbach 1978a). Typical taxa include the Cape Golden Mole (*Chrysochloris asiatica*) (Meester 1965). Several other endemic animal species occur, including the rare geometric tortoise (*Psammobates geometricus*). Approximately 11 664 km<sup>2</sup> or 16,7% of the Fynbos Biome is conserved (Table 7). There are 13 areas each of biome dimension totalling 9 521 km<sup>2</sup> or 13,6% of the Biome (Table 8). The Fynbos Biome, therefore, has the largest proportion of areas of biome scale conserved in South Africa (Table 8).

The Fynbos Biome is more severely invaded by alien plant species than the other biomes (MacDonald 1984). These are mostly woody plants and include *Acacia cyclops* A. Cunn. ex G. Don and *Acacia saligna* (Labill.) Wendl. on the coastal forelands and *Hakea sericea* Schrad. on the mountains. Although it has sometimes been suggested that the Fynbos Biome is particularly susceptible to invasion by alien plants, it has also been suggested that the high level of invasion may relate to the longer period of exposure to invasion in the biome (MacDonald 1984). There are fewer successful alien animal invaders in the Fynbos Biome. One of the more prominent species is the Argentinian ant (*Iridomyrmex humilis*) which disrupts

seed dispersal patterns and decimates indigenous populations of ants.

The suggested main subdivision of the Fynbos Biome is, as in the other biomes, based on moisture. The biome can be divided into two main sections, namely, 1, the lower rainfall areas of the coastal forelands, the mountain renosterbosveld of the Fynbos Biome and the arid fynbos and 2, the higher rainfall areas of the uplands and mountains. The border between these two divisions lies between the 450 and 550 mm isohyets. This division results in a particularly diverse lower rainfall unit in terms of floristic affinities and soil types, but ensures that there is greater uniformity within the unit in terms of main limiting factors and energy flow.

Various aspects of the Fynbos Biome have been researched for longer than the other biomes in southern Africa due to a longer research history. The research effort gained impetus with the establishment of the first two universities in southern Africa. More recently, the multidisciplinary co-operative Fynbos Biome Project was initiated to co-ordinate research on the natural systems in the biome. Main centres of research are Stellenbosch and Cape Town and the main organizations are the Directorate of Forestry of the Department of Environment Affairs and the University of Cape Town. About 20% of published papers on fire research in South Africa concerned Fynbos (Scott 1984). The specific characteristics of the biome have also attracted many overseas researchers over the years.

Economic utilization of fynbos vegetation is mainly limited to selective grazing by small stock on newly burned lowland areas and to wild flower production. The carrying capacity is very low and most grazing is obtained from cultivated fields and is only supplemented from natural vegetation. Anything but very young fynbos vegetation is remarkably unpalatable (Rutherford 1981). Wild flower production includes those picked wild and those cultivated. Most commonly utilized are members of the Proteaceae for which there is an important export market in the fresh or dried state. Important species are *Protea neriiifolia* R. Br., *Protea repens* (L.) L., *Protea compacta* R. Br. and *Protea magnifica* Link. Other less important uses of fynbos include production of Rooibos tea [*Aspalathus linearis* (Burm. f.) Dahlg.] and Buchu [*Agathosma betulina* (Berg.) Pillans] which is used to supply one of the world's most expensive volatile oils to the pharmaceutical industry. High quality thatching material is obtained from various species of Restionaceae, for example *Thamnochortus insignis* Mast.

The larger part of the coastal forelands is under cultivation. Almost all the coastal Renosterbosveld, which occurs on heavier soils, has been ploughed to wheat. Other important produce includes grapes, wine and deciduous fruits as well as a variety of other crops such as olives. Timber plantations are found on moist mountain slopes but are usually fairly isolated. Main species include *Pinus radiata* D. Don and *Pinus pinaster* Aiton.

The Fynbos Biome contains the major metropolitan area of Cape Town which is the oldest urban area in southern Africa and which, together with its satellites, covers an extensive area of the coastal forelands. In contrast, the mountain fynbos areas are remarkably undeveloped. These areas have invaluable recreational attraction. Tourism is usually centred around the natural scenic attractions of the area with its topographic diversity and proximity of mountains to sea. The floristic diversity and attraction in the biome is internationally renowned and is effectively displayed in the internationally popular botanic garden at Kirstenbosch, Cape Town.

The Fynbos Biome is poor in mineral resources. Main mineral deposits are kaolin, limestone, manganese and bentonite. Prior to urbanization in the Fynbos Biome, the area was settled by Khoi-khoi (Hottentots) and San (Bushman) tribes who were pastoralists and hunters respectively. Both employed fire to either improve grazing or to attract animals.

#### 4.5 Grassland Biome

The term grassland is well established, is effectively descriptive and is preferred to the vernacular grassveld, because of the former's local and international acceptance. The Grassland Biome is found mainly on the high central plateau of South Africa, inland areas of the seaboard of Natal and mountain areas of the south-eastern Cape Province. The area of the biome is 343 000 km<sup>2</sup> or 16,5% of South Africa (Table 3). Topography is mainly flat to rolling but can also be mountainous. Altitude is from 300 m on the coastal plateau to 2 850 m above mean sea level in the Drakensberg. East of the escarpment, the landscape is much dissected with many incision breaks.

The main geological units are the Beaufort and Ecca Groups followed by the Molteno, Elliot and Clarens Formations, all of the Karoo Sequence, and the Ventersdorp Supergroup. Other units include: Quaternary and Tertiary deposits; the Drakensberg Group and Dwyka formation, both of the Karoo Sequence; the Table Mountain Group of the Cape supergroup; the Pretoria, Chuniespoort and Wolkberg Groups of the Transvaal Supergroup; the Witwatersrand Supergroup and Dominion Group; the Swaziland Supergroup; the Rustenburg Layered Suite of the Bushveld Complex and older Basement complexes. The small area of the Witwatersrand Supergroup and Dominion Group are chiefly limited to the Grassland Biome.

The eastern escarpment forms the watershed between Atlantic and Indian Oceans. Major rivers draining into the Atlantic Ocean are the perennial Vaal, Caledon and Orange Rivers. Many rivers drain into the Indian Ocean, including the Tugela, Pongola, Umzimvubu and Kei.

The most common soil group in the Grassland Biome, accounting for just under 50% of the area, is the red-yellow-grey latosol plinthic catena. This is followed by combinations of black and red clays and solonetzic soils, freely drained latosols and black clay soils. These

freely drained latosols and black clay soils are mainly limited to the Grassland Biome. Other soil groups include undifferentiated rock and lithosols, lime-poor weakly developed soils on rock and undifferentiated swamps and alluvial plains. The acid soils of the red-yellow-grey plinthic catena are better represented in the Grassland Biome than the other biomes.

Soil erosion in the Grassland Biome is limited in the higher rainfall areas due to the high vegetation cover. However, where vegetation cover is reduced through veld mismanagement, erosion can be severe, especially on steeper slopes and erodible solonetzic, duplex soils such as are found in Natal.

The Grassland Biome is limited to the summer and strong summer rainfall areas with mean annual rainfall mostly between 400 and 2 000 mm. Frosts are common and mean lowest minimum temperature for the coldest month is generally consistently below +1°C. The cold is exacerbated by aridity or increasing altitude. The length of the period in which frost can occur is generally between 30 and 180 days (Schulze, B.R. 1965). In some grassland at higher altitude, cryoturbation results in small bare patches such as the well known terracettes of the Drakensberg (Killick 1963). Occasional fog occurs and is most frequent along the upper escarpment and seaward scarps, where hygrophilous mist belt vegetation is supported. The average number of days with thunder is higher than in the other biomes and is usually much more than 30, averaging about 70 for the biome (Schulze, B.R. 1965). Lightning flash densities to ground are also highest (Edwards 1984). This biome has the highest hail frequency for a given point and is generally greater than five hail storms per year (Schulze, B.R. 1965). The Grassland Biome is the only biome that corresponds to a single unit in Köppen's classification of climate, namely Cwb (Schulze & McGee 1978).

The vegetation of the Grassland Biome is physiognomically monolithic and is characterized by strong dominance of hemicryptophytes of the Poaceae. Canopy cover is moisture dependent and decreases with lower mean annual rainfall. Grazing has a decisive influence on canopy structure. Where trees occur these are associated with local specialized niches, for example, in Bankenveld (Veld Type 61 of Acocks 1975) and higher altitude areas east of the escarpment.

The vegetation of the Grassland Biome follows a rainfall gradient which generally corresponds to the relative contributions to the plant cover by 'sweet' and 'sour' grass plants. 'Sweet' grasses, in contrast to 'sour' grasses, usually have a lower fibre content, maintain a higher above-ground nutrient level into winter and tend to be more palatable to stock. In the area with mean annual rainfall above about 625 mm (moist), sour grasses (e.g. *Aristida junciformis* Trin. & Rupr.) tend to predominate. In areas below 625 mm (dry), sweet grasses (e.g. *Panicum coloratum* L.) are more common, but they are seldom dominant, as they can be in parts of Savanna, which has a lower rainfall than in the Grassland Biome. Although many of the sour or intermediate grasses are

better represented in the Grassland Biome than in Savanna, the sweet grasses in the Grassland Biome are often better represented in Savanna. The 625 mm isohyet also corresponds to the lower limit for increased plant yields with application of nitrogen and phosphorus (Tainton 1981). The soils of the moist grasslands are usually more leached by the higher rainfall and tend to be dystrophic in comparison with the generally eutrophic soils of the dry grasslands. In moist grassland various exceptions occur, usually on turf soils e.g. on patches in the eastern highveld and on the Drakensberg Basalts. The moist grassland contains a climatically marginal variation on the savanna border east of the escarpment. In this area minimum temperatures are higher than in the rest of the biome and there is potential for localized phanerophytic occurrence. Such climatically marginal variations correspond to 'false grassland' (Acocks 1975; Mentis & Huntley 1982; Huntley 1984), the extent of which is often much exaggerated. Although some woody plants may have occurred in these areas in the past, grassland is maintained by biotic factors such as persistent wood removal and indiscriminate use of fire over the centuries. Probably the most noteworthy species with wide distribution in the Grassland Biome is *Themeda triandra* Forsk. C<sub>4</sub> grasses tend to predominate in the Grassland Biome except in the high Drakensberg area where C<sub>3</sub> can also be important (Vogel *et al.* 1978). The number of rare plants in the Grassland Biome is not particularly large but increases in the wetter areas and mainly includes non-graminoid plants (Hall *et al.* 1980). Succession after disturbance where the grassland plant community is no longer in equilibrium with its environment, usually involves therophytes in the initial stages followed by establishment of perennial grasses. Grazing management can greatly influence composition of grassland. It is particularly in the zone of niche overlap between sour and sweet grass species that such management is most effective in maintaining a favourable balance between these plant groups. In high rainfall sourgrassland, environmental conditions are inimical to most sweet grasses and grazing management can not be expected to change the basic sour status of this grassland type. The grass plant is well adapted to defoliation such as by grazing, fire or mowing. The tillers of the grass plant are the fundamental unit of the plant. Although individual tillers are usually annual, the ability of the plant to produce a succession of lateral daughter tillers enables the plant to be perennial under conditions of defoliation. The lateral daughter tillers are also capable of producing their own root systems. Upright tillers are found in tufted grasses, whereas horizontal tillers are found in rhizomatous grasses (below-ground tillers) and in stoloniferous grasses (above-ground tillers). Rhizomatous species are least influenced by trampling. The basal meristems of grass leaves enable regrowth after defoliation and draw on carbohydrate reserves from stem bases or rhizomes. Although the above adaptations to defoliation are highly effective, excessive or very frequent defoliation depletes reserves with adverse consequences, especially in dry areas.

Above-ground plant production varies from about 1 000 kg ha<sup>-1</sup>a<sup>-1</sup> in drier areas to about 6 000 kg ha<sup>-1</sup>a<sup>-1</sup> in the warm wetter areas. The frequency of fire in grassland depends on production and fire is least frequent in the drier areas but in the moister areas can occur annually. Geophytes generally flower in spring but flowering is stimulated by fire during the warm moist time of the year. The absence of defoliation usually leads to the demise of geophytes (Tainton & Mentis 1984).

In the past, blesbok (*Damaliscus dorcas phillipsi*), black wildebeest (*Connochaetes gnou*) and springbok (*Antidorcas marsupialis*) were abundant. Species in common with the Nama-Karoo Biome include the black-footed cat (*Felis nigripes*). Thirty three percent of the mammal species of southern Africa occur in the biome of which only 3 species are endemic (Rautenbach 1978a). Bird densities range from 50 to 370 birds per 100 ha and include a wide range of species (Winterbottom 1978). Typical species include the blue crane (*Anthropoides paradisea*) and blue korhaan (*Eupodotis caerulescens*). Despite the relatively high rainfall of the Grassland Biome, molluscs are poorly represented to absent (Van Bruggen 1978) possibly as a result of frequent surface fire.

Approximately 3 520 km<sup>2</sup> of the Grassland Biome is conserved, which is 1,12% of the area of the biome (Table 7). Conserved areas of minimum biome area are limited to two, both of which are of marginal biome dimension owing to shape (Table 8). Alien plant species have not invaded much of the area of the Grassland Biome outside streambank habitats (Henderson & Musil 1984). The main woody plant invaders are wattles (*Acacia* spp.). More important herbaceous alien invader species in the Grassland Biome appear to favour moist habitats and include the cultivated pasture species such as *Paspalum dilatatum* Poir., *Paspalum urvillei* Steud. and *Pennisetum clandestinum* Chiov.

The Grassland Biome may be divided (see effect of rainfall gradient above) into two major natural divisions based on moisture availability: 1, Moist grassland constitutes by far the greater part of the biome; sour unpalatable grasses predominate; soils tend to be leached and dystrophic; plant canopy cover and production are high and frequency of fire is higher; 2, Dry grassland\* is found in areas where sweet palatable grasses are more common; soils tend to be less leached and eutrophic; plant canopy cover, production and frequency of fire are lower. The border between moist and dry grassland is best expressed as ranging between the 500 and 700 mm isohyet.

Much research has been carried out on the vegetation of the Grassland Biome. Five major universities are situated in this biome. Each has conducted much research on grassland, often emphasizing agriculture, especially at the universities with Agriculture Faculties. There is a

\* Not to be confused with the sub-biome 'arid grassland' areas in the Nama-Karoo and Succulent Karoo biomes.

long history of research programs on grassland at the University of Natal (Pietermaritzburg) and at Frankenwald (University of the Witwatersrand). Owing to the important economic nature of grasses, the Department of Agriculture and Water Supply has established many major experimental farms in this biome in which intensive and extensive research has been conducted for many decades. The Departmental emphasis on the Grassland Biome is also shown by having five of the seven agricultural regions in South Africa include parts of this Biome. Other organizations concerned with grassland research include, the Directorate of Forestry, Department of Environment Affairs, the National Parks Board and the Natal Parks Board. The various research projects are co-ordinated as part of the Grassland Biome Project under auspices of the CSIR. About 54% of published papers on fire research in South Africa concerned the Grassland Biome (Scott 1984). Despite the large research effort in grasslands, syntheses of the full range of information are lacking.

The Grassland Biome is very important for dairy, beef and wool production. Carrying capacity varies from 5 ha/AU\*\*/annum in the drier areas to 1,75 ha/AU/annum in moist grasslands (Tainton 1981). Cultivation of crops is very important in the biome which contains the whole maize triangle of South Africa — this crop is the most important in the biome. Other important crops include, sorghum, wheat, sunflowers and cherries. Planted pastures occur in the higher rainfall areas and include cocksfoot, clover, lucerne and stargrass. Silviculture is generally limited to areas with mean annual rainfall greater than about 890 mm but seedlings need to be protected from frost (Grut 1965). Main species are Black Wattle (*Acacia mearnsii* De Wild) and *Pinus patula* Schlechtd. & Cham.

The Grassland Biome contains the greatest concentration of urban areas in southern Africa, namely the Witwatersrand complex with population exceeding 2 million. Other major centres include Bloemfontein and Pietermaritzburg. The urban population density in the Grassland Biome is greater than that in any other biome. Tourism is centred on the scenic grandeur of the eastern escarpment and attractions of the major urban areas including the world's deepest mines. The main economic reserves of the biome are gold, coal, diamonds, uranium and aluminium. Other important deposits include: silver, iron, bentonite, platinum, titanium, zirconium, rare earths, thorium, manganese, fluorspar, barytes, chrysotile, nickel, tin, beryllium, tantalum, lithium, limestone, sulphur, dolomite, flint and refractory.

Burtt Davy (1905/6) observed that Black tribes were practically 'exotic' to the area of the Grassland Biome. This may relate to lack of wood for fuel and construction and dislike of the cold winters. The surrounding savanna was found to be more suitable with regard to availability of wood and mild winters.

#### 4.6 Nama-Karoo Biome

Divergent political histories make it difficult to find a single, traditionally accepted term for this biome. The term Nama-Karoo is a concatenation of Namaland of southern South West Africa/Namibia and the Karoo of South Africa. Karoo (formerly spelt Karroo) is derived from the Hottentot word 'Kuru' (Nienaber & Raper 1977, quoted Van der Walt 1980) or 'Karu' (Vorster & Roux 1983) meaning dry, barren land and is traditionally, mainly limited to dry areas of the Cape Province. The term Karoo is therefore also retained within the name Succulent Karoo Biome which includes Namaqualand (of the Cape) but excludes Namaland (of South West Africa/Namibia) (Philip's New World Atlas 1983). The South West African/Namibian part of the Nama-Karoo Biome is called the 'Karoo Shrub and Grass' vegetation type by Giess & Tinley (1968) and the 'Great Nama Desert' by Phillips (1957). The floristic differences between the central east Karoo and Namaland have possibly dissuaded botanists from proposing a single name for this area despite the similarities, for example in the dominant *Rhigosum trichotomum* in Namaland and in large parts of the upper Karoo (Acocks 1975).

The Nama-Karoo Biome is found on the central plateau of the Cape Province, north of the east-west Cape folded mountain belt, the south-western Orange Free State and the southern interior of South West Africa/Namibia. Smaller parts occur in the eastern Cape interior, Lesotho and the interior margin of the central Namib Desert in South West Africa/Namibia. The biome is the second largest south of 22°S and covers an area of about 541 000 km<sup>2</sup>. Most of the area consists of extensive, even to undulating plains, interdispersed with mesas, hills or, occasionally, mountains. Height above sea level ranges from about 500 to 2 000 m but with most of the area lying between 1 000 and 1 400 m. The area of the biome in Lesotho is between 2 850 and 3 400 m above sea level. Further discussion of this anomalous part of the biome is reserved for the end of this section.

The main stratigraphic units are the Beaufort and Ecca Groups and Dwyka Formation of the Karoo Sequence followed by the Fish River and Schwartzrand Subgroups, Nama Group, Damara Supergroup and older Basement complexes. Other units include: Quaternary and Tertiary deposits; the Drakensberg and Lebombo Groups of the Karoo Sequence; Kuibis Subgroup, Nama Group, and Sinclair Group, both of the Damara Supergroup; Abbabis and Kheis Groups; Waterberg Group; Olifantshoek, Postmasburg, Campbell and Griquatown Groups of the Griqualand West Supergroup; the Ventersdorp Supergroup; and younger Basement complexes. The small area of the Sinclair Group is limited to this biome.

The main drainage basin of the biome is that of the Orange River which includes the partly deeply incised Fish River tributary. Many of the water courses are seasonal. The Orange River has perennial water owing to its head water area lying in higher rainfall areas outside

\*\* One AU (e.g. cow) is taken as 5 ssu (e.g. sheep).

the biome. Other main drainage basins include that of the Fish (eastern Cape) and Gamka which drain to the Indian Ocean. In parts of the central-upper Karoo, large pans occur.

The most common soil group in the Nama-Karoo Biome, accounting for over 80% of the area in South Africa, is lime-rich, weakly developed soils on rock. Other soil groups include sands, combinations of red clays and solonetzic soils, and undifferentiated rocks and lithosols. The soils are generally alkaline (pH 7,0 to 8,3) (Vorster & Roux 1983). Accumulation of silt or clay is common in depressions and pans. Many of the soil surfaces of the Nama-Karoo area are easily eroded by water and wind. Particularly where vegetation cover has been reduced by persistent overgrazing, erosion of soil has reached an advanced level of degradation in many parts. Where the sand veneer of some areas of arid grassland is eroded away, dwarf shrubs invade (Tinley 1977). Despite the erodability of the soil, the ratio of Mean Annual Runoff to Mean Annual Precipitation averages less than 5% and is an order of magnitude less than for South African humid catchments (Görgens & Hughes 1982).

The biome is limited to strong summer, summer and even rainfall areas. The Summer Aridity Index (SAI) of the biome within its original limits is between about 3,6 and 5,1 but in the area invaded by Nama-Karoo elements, SAI can be as low as 3,1. Mean annual rainfall for most of the area ranges from about 100 to 520 mm. Minimum temperatures are low with frequent frost in winter and mean lowest minimum temperature for the coldest month ranges from about 0°C to less than -9°C. The length of the period in which frost can occur is between 30 and 180 days. The whole biome has an average annual duration of bright sunshine of greater than 70% of that possible (Schulze, B.R. 1965) which distinguishes it from the other biomes of southern Africa.

The vegetation of the biome is dominated by chamaephytes and hemicryptophytes and can be described as a grassy, dwarf shrubland (Edwards 1983). The hemicryptophyte component makes an apparently low contribution in many parts but this is usually an unstable condition maintained by grazing pressures. The ratio of hemicryptophyte to chamaephyte production is usually lowest on 'shale-veld' and highest on 'leegte-veld' (in depressions) (Viljoen & Immelman, quoted Vorster & Roux 1983). A high ratio is found in the eastern area of invasion under conditions of protection from grazing. Areas with such very high ratios, namely arid grassland, along the desert margin and in Bushmanland are closely associated with sandy substrates of sub-biomic proportion. With removal of the sand through erosion, chamaephytes increase and the ratio decreases appreciably.

Karroid shrub communities extend north of 22°S along a narrow inland margin at the base of the western escarpment in South West Africa/Namibia (Heydorn & Tinley 1980). The hemicryptophytes of the biome are mainly C<sub>4</sub> graminoids (Vogel *et al.* 1978). Plant species diversity and number of rare and endangered species in

the biome are relatively low (Hall *et al.* 1980).

Plant adaptation to drought in the biome is more through drought tolerance than through drought avoidance by, for example, storage of water, or through drought evasion. Many of the chamaephytes are facultatively deciduous in response to the high temporal variability of rainfall. Various plant groups are also adapted to grow at different times of the year but with both dominant groups experiencing a slackening of growth with high midsummer temperatures (Vorster & Roux 1983). Succession of plant composition in the biome is usually taken to start after disturbance by overgrazing. The usual progression, given a significant reduction in grazing pressure and a suitable distribution of rainfall (Vorster & Roux 1983), is a steady increase in hemicryptophyte cover and a more variable decrease in chamaephyte cover.

Above-ground primary production of around 3 000 kg ha<sup>-1</sup> a<sup>-1</sup> can be attained in the highest rainfall parts of the biome, but for large areas of the biome, it is between only 500 and 1 500 kg ha<sup>-1</sup> a<sup>-1</sup>. Above-ground (dry) biomass for most areas ranges from about 1 to 7 metric tonnes ha<sup>-1</sup>. The amount and nature in the fuel load of the vegetation is generally inadequate for carrying fire and fire is consequently rare. Only in the more moist north-eastern and mountainous parts is fire more frequent and employed to control numbers of undesirable grazing shrubs, such as *Chrysocoma tenuifolia*.

The former vast herds of springbok (*Antidorcas marsupialis*) no longer occur in the biome. The few endemic or near-endemic bird species include Sclater's Lark (*Spizocorys sclateri*). Most arid zone birds can drink saline water and can excrete high concentrations of salt by water resorption in kidneys or cloaca and/or by salt excretion via the salt gland (Maclean 1974). Large outbreaks of economically damaging insect pests occur. One of these is the Karoo caterpillar (*Loxostega frustalis*) for which the common Karoo chamaephyte genus *Pentzia* serves as main host plant (Möhr, quoted Vorster & Roux 1983). The main swarming area of the brown locust (*Locusta pardalina*) is the Nama-Karoo Biome (Lea 1964) and in the transitional southern Kalahari area, this locust is characteristic of the Karroid areas, distinct from the surrounding (savanna) vegetation (Barker 1981).

The conserved area of the biome is very small and only recently has increased to about 0,7% of the area of the biome in South Africa (Table 7). For the whole biome south of 22°S, this percentage remains less than 1%. The number of alien invasive plant species in the biome are few. Most important is probably the prickly pear (*Opuntia aurantiaca*) in the south-eastern parts. Indigenous invasive species are important in the more mesic eastern parts and include *Chrysocoma tenuifolia*.

The main body of the Nama-Karoo Biome may be subdivided primarily on the basis of mean annual rainfall into two parts of unequal area: a small part with relatively high rainfall corresponding to those areas formerly covered mainly by grassland (the truly 'false' and irrevers-

ible Karoo); and the vast majority of the area with lower rainfall.

Research on the biome has been limited by the lack of any university in the biome. However, a long history of fruitful research has emanated from the Grootfontein station of the Department of Agriculture and Water Supply in Middelburg. More recently, a co-operative research program, the Karoo Biome Project, has been launched with main input from Grootfontein, the University of the Orange Free State and Universities of the eastern Cape Province. All these centres are at or near the eastern extremities of the biome and, consequently, less attention is usually given to the other parts of the biome.

Most of the biome is used for grazing purposes, primarily through sheep for production of mutton, wool and pelts (Karakul). Goats are also important in some areas. Carrying capacity differs according to region and is around 1 ha/ssu in the more moist east to over 5 ha/ssu in arid Bushmanland (Baard 1978). Cultivation of crops in the biome is usually strictly limited to small areas where irrigation is possible. Urbanization within the biome is limited to medium-small towns and villages, several of which have recently exhibited negative population growth rates ascribed to the drift to larger centres outside the biome. Main centres in the biome include Upington, Keetmanshoop, Beaufort-West and Middelburg. Tourism potential for much of the biome is relatively low, given the monotony of the vast plains. However, some tourism value is found in the topographically more diverse parts of the Orange River Valley and mountain areas, especially of the escarpment. Various odd features, such as the stone pillar of the Mukorab, north of Keetmanshoop, are also attractions.

The biome contains medium or larger deposits of uranium, lead, zinc, beryllium, tungsten, copper, gypsum, barytes, sillimanite, feldspar, fluorspar, nickel, iron, vanadium, titanium, silver, tantalite, sulphur and lithium. Smaller deposits of many other minerals occur.

The status of the disjunct high altitude outlier of the Nama-Karoo Biome on the Drakensberg escarpment is undisputed in terms of the accepted definition of a biome. Despite some similarities between this outlier and the rest of the biome, there are also several associated differences. Main similarities are in life form dominance and a qualified interpretation of climate where the physiological drought experienced by high altitude plants tends to offset effects of the higher rainfall. However, temperatures are more extreme with lower minima, wind is more important and lightning flash densities are at least double that in the remainder of the biome i.e. greater than 8 flashes  $\text{km}^2 \text{ a}^{-1}$  (Edwards 1984). The floristic affinities of much of the vegetation is altogether different and is allied to the temperate montane extension of Cape fynbos taxa, e.g. *Erica*. Grasses are usually not  $C_4$  but  $C_3$ . Plant productivity is probably somewhat higher than most of the remainder of the biome and fire is more frequent. The more severe winter temperatures are likely to dictate different

zoological components compared to most of the remainder of the biome. Conservation status is virtually nil. Alien invasive plant species appear to be absent. The research effort on the high Drakensberg has been mainly directed at the higher rainfall parts and not the drier leeward side. More research is needed. Much of the area is heavily utilized for small stock grazing. Mineral resources are very low except for occurrence of some diamondiferous kimberlite.

#### 4.7 Savanna Biome

The term savanna, once restricted to describe central South American grasslands in Spanish, is now widely accepted as describing vegetation with a herbaceous, usually graminoid, layer with an upper layer of woody plants, which can vary from widely spaced to 75% canopy cover (Edwards 1983). In the latter case savanna is often referred to as woodland.

The savanna biome extends from north of 22°S into central South West Africa/Namibia, Botswana, higher rainfall areas of the northern Cape, the northern two-thirds of the Transvaal, lower altitude areas of the north-western Orange Free State, Mozambique, central and east Swaziland, lower altitude areas of Natal, Transkei and the eastern Cape Province, and certain belts in the southern Cape. The biome does not only have the greatest extent in southern Africa but is the largest, comprising about 959 000  $\text{km}^2$  or 46.2% of southern Africa (one third of South Africa, Table 3). Most of this area is on the extensive plains of the Kalahari Basin and coastal platform of Mozambique/Tongaland. More rugged topography is found on or against the western and eastern escarpments and on valley slopes along the east coast and parts of the southern Cape. Altitude varies from coastal to a maximum that depends on latitude. This maximum can vary from a few hundred metres in the south to 2 000 m above sea level in the north.

Almost all the major stratigraphic units of southern Africa occur in the Savanna Biome. The main units are Quaternary and Tertiary deposits followed by Basement complexes. Other units include: Cretaceous deposits; all the units of the Karoo Sequence and the Cape Supergroup; Schwartzrand and Kuibis Subgroups, Nama Group, Damara Supergroup; Swakop, Malmesbury, Nosib and Rehoboth Groups of the Damara Supergroup; Abbabis, Kheis, Waterberg and Soutpansberg Groups; all Groups of the Transvaal and Griqualand West Supergroups; Ventersdorp and Swaziland Supergroups; Salem Granite; alkaline igneous rocks; and all suites of the Bushveld Complex. The small area of Nosib and Rehoboth Groups and the greater portion of the Bushveld Complex are limited to this biome. Major drainage basins are the Limpopo to the Indian Ocean and those of the Kalahari Basin (e.g. the seasonal Nossob and Molopo) which do not reach the oceans. Many other shorter rivers pass through the biome, especially along the east coast.

The most common soil group in the Savanna Biome, accounting for just under 25% of the area in South

Africa, are weakly developed soils on rock closely followed by sands, combinations of black and red clays and solonetzic soils, and generally neutral soils of the red-yellow-grey latosol plinthic catena. The red clays and combinations of black and red clays are mainly limited to the Savanna Biome. Other soil groups include undifferentiated rocks and lithosols, freely drained latosols, undifferentiated swamps and alluvial plains, as well as undifferentiated red porous soils and lithosols on limestone. All the major soil groups of South Africa occur in the Savanna Biome. Low rainfall savanna soils tend to be base rich and calcrete can be common. High rainfall savanna soils tend to be dystrophic and laterites are common.

Most of the Savanna Biome occurs in the summer and strong summer rainfall areas with a Summer Aridity Index (SAI) less than 4,0 and mean annual rainfall of above 235 mm. A relatively small area, with predominantly succulent plant form, extends into an area with mainly even rainfall, higher summer aridity (SAI up to 5,0) and mean annual rainfall which can be below 235 mm. Savanna has the greatest range of temperature minima. It is absent from high rainfall areas with low winter temperature minima but not from low rainfall areas with relatively severe winter frosts. Length of the period in which frost can occur, is up to 120 days. The biome has summers of longest duration and has the widest range in duration of summer, from less than 6 months to more than 7½ months (Schulze 1965). The biome has generally much fewer than five hail storms (for a given point) per year which is fewer than that for the adjacent Grassland Biome.

The codominant life forms at biome scale are hemicryptophytes and phanerophytes. The most common hemicryptophytes are graminoids of the C<sub>4</sub> type, with C<sub>3</sub> types also important in the southern and eastern Cape savanna areas (Vogel *et al.* 1978). The phanerophytes are more variable. Although extensive stands of phanerophytes just over 1 m or almost 20 m tall exist in places, phanerophytes of most of the savanna in southern Africa are between 3 and 7 m tall and are often multistemmed and the areas are referred to locally as bushveld. Phanerophytes may be locally dominant, for example, where overgrazing has led to severe bush encroachment or in parts of the eastern Cape savanna which contain dwarf forests of sub-biomic proportion. In certain areas, the phanerophyte component is succulent, being dominated by species such as *Portulacaria afra* Jacq. or *Euphorbia ingens* E. Mey. ex Boiss. These areas of succulence differ from those of the Succulent Karoo Biome and from the succulent parts of the Nama-Karoo Biome in their larger plant size. They also differ from the Succulent Karoo Biome in terms of importance of graminoid hemicryptophytes, lower species diversity and rainfall seasonality. Plant species diversity, in the Savanna Biome may be classed as average relative to that of the other biomes. The high species number in the biome is mainly a function of the size of the biome. Most of the biome's flora falls within the Palaeotropical Kingdom (Good

1964). The biome contains a number of plant species of unusual form, such as the large bottle-tree form, *Adansonia digitata* L. The biome also includes the Valley Bushveld which is the veld type (Acocks 1975) containing the greatest range of rainfall seasonality from even to strong summer in South Africa. Areas of *Brachystegia* miombo occur north of the Limpopo River in Mozambique (Werger & Coetze 1978).

Many other features such as bush clumps and treeless dambos occur over large areas of savanna. Although it is tempting to see more variation in areas of great extent such as the Savanna Biome, it is appropriate to quote Adamson (1938) verbatim for the savanna areas from the eastern and northern Cape northwards to the Sudan 'A vegetation that covers so wide an area of course exhibits great diversity in detail from place to place, but not only are the main structural features the same throughout, the essential characters of the climate are also the same'.

The plants of most of the biome are well adapted to withstand fire. Fires are usually surface fires and mortality of both phanerophytes and hemicryptophytes after fire is remarkably low, often less than 10% mortality. In terms of fire life forms there is a simple correspondence of phanerophytes to fire-phanerophytes and hemicryptophytes to fire-hemicryptophytes. Only chamaephytes correspond differently to fire-hemicryptophytes (Fig. 19). The relationships between life form and fire life forms in savanna differ greatly from those in the Fynbos Biome (Fig. 18). Even where savanna phanerophytes experience top kill, many resprout from the base. The age of main below-ground plant parts can be several times that of the above-ground parts. The remarkable persistence of the dominant life form plants means that the system is less dependent on regular recruitment through seedlings which can be delayed until favourable conditions occur. As with fire, the dominant life forms are well adapted to withstand drought although the woody plants usually have a higher resistance than the hemicryptophytes. The difference is usually exacerbated by increased grazing pressure on the hemicryptophytes during drought. It is possible that without regular fire, large parts of savanna would not be maintained as two clearly codominant layers of hemicryptophytes and phanerophytes.

Above-ground primary production varies from about 1 000 kg h<sup>-1</sup> a<sup>-1</sup> in arid areas to 7 000 kg ha<sup>-1</sup> a<sup>-1</sup> on optimum sites. Above-ground (dry) biomass depends to a large extent on the proportion of woody plants and varies from 5 metric tonnes per hectare in open shrubby savanna to between 45 and 60 t ha<sup>-1</sup> in some savanna-woodland or thicket. Herbaceous layer biomass of more than 2 t ha<sup>-1</sup> can usually readily carry a surface fire. Consequently, annual fires are possible in higher rainfall areas with woody plant canopy cover usually less than 40%. Annual fires are rare in arid savannas where productivity is low and insufficient fuel accumulates over years.

Several bird species are typical of the Savanna Biome and include *Turtur chalcospilos*, *Corythaixoides*

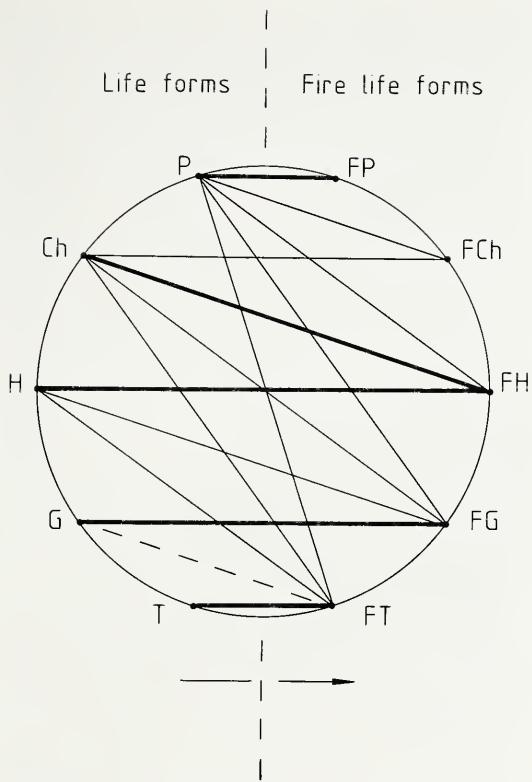


FIG. 19.—The relationship between life forms and fire life forms in the Savanna Biome shown by bold lines. Abbreviations used are: P, phanerophytes; Ch, chamaephytes; H, hemicryptophytes; G, geophytes; and T, therophytes.

*concolor*, *Otus senegalensis*, *Coracias caudata* and *Tockus flavirostris*. Mammals include the kudu, *Tragelaphus strepsiceros*, whose current southern distributional limits correspond to most of the southern limits of the biome. The Savanna Biome is the area where many of the big game species, for example, lion (*Leo leo*), buffalo (*Synacerus caffer*) and elephant (*Loxodonta africana*) may still be found, usually in reserves. The great majority of southern African anurans are savanna-living (Poynton & Broadley 1978). There is a high reptilian species diversity which includes the black mamba (*Dendroaspis polylepis*). In contrast, savanna contains little molluscan life (Van Bruggen 1978). Termites, such as *Macrotermes natalensis*, are important in savanna. Malaria parasites (*Plasmodium* spp.) occurred in much of southern African savanna south to southern Natal but has been much reduced by spraying programmes against the vectors, namely mosquitoes of the genus *Anopheles*.

The conservation status of the biome is good with 8.5% of the area conserved in South Africa (Table 7) and includes three individual areas in excess of 1 000 km<sup>2</sup> which include the 19 485 km<sup>2</sup> of the Kruger National Park (Table 8). In southern Africa, the relatively high conservation percentage is maintained, especially through the even larger Gemsbok and Central Kalahari Parks of Botswana (Huntley 1978). Invasive alien plants are generally only locally important in savanna, for example,

*Prosopis chilensis* (Mol.) Stuntz in the arid savannas and various species along water courses and parts of the Indian Ocean coastal belt.

It has become widely recognized that the Savanna Biome in southern Africa can be divided into two main subtypes namely arid, base rich savanna with mean annual rainfall typically below 650 mm, and moist nutrient poor savanna (Huntley 1984) with mean annual rainfall above 530 mm. In terms of the accepted biome definition these types cannot be raised to full biome status. The graminoid hemicryptophyte component of arid savanna tends to have less lignin, a higher nutritional value and palatability to grazing stock and is often classed as 'sweetveld'. The phanerophyte component often comprises palatable species of the genus *Acacia*. The graminoid hemicryptophyte component of the moist savanna tends to have a higher lignin content, lower nutritional status and palatability in winter and is often classed as 'sourveld'. The phanerophyte component includes a wide range of taxa, the plant leaves of which have a high nutrient content but often low palatability to most browsing animals in savanna.

The Savanna Biome in southern Africa has experienced a considerable research effort which in the last decade has been given a major impetus through the South African Savanna Ecosystems Project, the first such programme to be administered by the Council for Scientific and Industrial Research (CSIR) of South Africa. This programme involved work by various universities and government research organizations on a single site in the northern Transvaal but has more recently diversified to numerous other sites. The programme has been recognized as one of the major research programmes on any world savanna system. About 16% of research papers devoted to effects of fire in South Africa concern the Savanna Biome (Scott 1984).

Most of the Savanna Biome is used for extensive grazing by stock animals, mainly cattle. Carrying capacity varies from 4 ha AU<sup>-1</sup> a<sup>-1</sup> in the moist savannas to 30 ha AU<sup>-1</sup> a<sup>-1</sup> in the drier areas (Tainton 1981). Parts of the biome are becoming increasingly used for game ranching where despite the difficulty of control of animal units, certain game animals, for example kudu, can utilize the woody plant component, have the ability to tolerate many plant toxins and can be run separately from or together with domestic stock to optimize utilization of both main plant components of savanna. Game trophy hunting is also incorporated into some game farming enterprises. In some areas of savanna, for example in the eastern Cape, goats are used as major consumers of woody plant browse material.

Where rainfall is adequate (usually more than 500 mm a<sup>-1</sup>) and soils are more fertile and arable, woody plants are often cleared and the land used for various crops such as sunflower, maize and groundnuts. The savanna areas most notably turned to crops are the higher rainfall areas of the arid savanna division of the biome (see above) such as the Springbok Flats of the Transvaal. Silviculture is usually limited to moist areas

close to the interface between the Savanna and Grassland Biomes.

Urbanization in the biome, apart from the marginal coastal cities such as Durban, Port Elizabeth, East London and Maputo, and others close to the Grassland Biome, for example Pretoria and Pietermaritzburg, is limited to smaller towns. Pietersburg and Windhoek are in relatively high altitude savanna, which taken together with the above, suggests that urbanization well within the borders of the Savanna Biome has been limited by high summer temperature and humidity and past threats of human disease.

Much of the tourist potential of the Savanna Biome is linked to wildlife appreciation, warm all year climate and appeals to a pioneering spirit. The structure of savanna vegetation is that closest to a parkland architecture which most developed countries have tried to simulate in their urban recreational areas. This structure optimizes the trade-off between ease of perambulatory movement and overhead protection for humans. Most current tourist use of the Savanna Biome is through game parks and reserves.

The Savanna Biome is rich in mineral resources. Medium and larger deposits that are being exploited include in descending order of size: chromium, iron, vanadium, manganese, limestone, fluorspar, refractory (flint), platinum group metals, andalusite, nickel, titanium, magnesite, diamond, phosphate, antimony, copper, tin, crocidolite, kaolin, beryllium, gemstone, dolomite, silicon, attapulgite/sepiolite, rare earths, kyanite, zinc, gypsum, barytes and anthophyllite.

The savanna areas have a record of very early human occupation (Clark 1980) and it has been hypothesized that the structure of savanna vegetation is maintained largely through this association. There is a strong traditional association between the Savanna Biome and the Black people. Even in terms of the current distribution of areas specifically set aside for Black tribes, more than 90% of these areas (in South Africa and South West Africa/Namibia) are in the Savanna Biome.

#### 4.8 Succulent Karoo Biome

The nomenclature of this biome is probably the most difficult to determine since no single regional, traditional name exists for the whole area. The nearest is 'winter rainfall Karoo' which, although applicable, is a purely climatic description in contrast to each of the other biomes where either vegetation or a traditional geographical term is stressed. The term Succulent Karoo is regarded as appropriate since, although by no means all the plants of the biome are succulent, succulence is a recurring feature at varying levels of abundance throughout the biome. The term should not be regarded as being limited to Acocks's (1975) 'Succulent Karoo' Veld Type No. 31.

The Succulent Karoo Biome is found mostly west of the western escarpment from the Lüderitz District of South West Africa/Namibia through the western belt of

the Cape Province, and inland of the Fynbos Biome to the Little Karoo. The biome covers approximately 111 000 km<sup>2</sup> which makes it the fourth largest biome in southern Africa after the Savanna, Nama-Karoo and Grassland Biomes. Much of the terrain is flat to gently undulating such as the west coastal platform, Knersvlakte and Tanqua Karoo. Hilly and more rugged topography occurs in Namaqualand, the Robertson and Little Karoos and parts of the western escarpment. The extreme altitudinal range is from sea level to about 1 500 m, but most of the area lies below 800 m above sea level.

The main geological unit is old Basement complexes followed by the Ecca Group and Dwyka Formation of the Karoo Sequence, Quaternary and Tertiary deposits, and the Garies Group of the Damara Supergroup. Other units include: Cretaceous deposits, the Beaufort Group of the Karoo Sequence; the Bokkeveld Group of the Cape Supergroup; the Schwartzrand and Kuibis Sub-groups, Nama Group, Damara Supergroup; Abbabis and Kheis Groups; Cape Granite Suite; and younger Basement complexes.

Largest drainage systems are the Tanqua–Doring–Olifants and the Gouritz and its relevant tributaries. Most others are small west-flowing systems, including a relatively short section of the Orange River and mouth. The majority of river courses in the biome contain short-lived seasonal rivers.

The most common soil group in the Succulent Karoo Biome accounts for just over 80% of the area in South Africa and is, as in the Nama-Karoo Biome, lime-rich, weakly developed soils on rock. Other soil groups include sands, undifferentiated alluvial plains and neutral soils of the red–yellow–grey latosol plinthic catena. In terms of major soil groups (MacVicar 1973), there is little difference between soils of the Succulent Karoo and Nama-Karoo Biomes.

Many of the soil types of the biome are readily erodable and there are many examples of deep gully and sheet erosion that has occurred in historical times due to overgrazing of the originally sparse vegetation cover. The generally low kinetic energy of rainfall in this biome, however, slows the rate of erosion.

The Succulent Karoo Biome is mainly limited to the even, winter and strong winter rainfall areas with greatest summer aridity in southern Africa. SAL ranges from 4,8 to about 7,5 and mean annual rainfall from approximately 20 to 290 mm. In terms of mean annual rainfall, therefore, the biome overlaps with that of the Desert Biome. Areas with mean annual rainfall below 50 mm are found in the far northern coastal section adjoining the Desert Biome, whereas areas with mean annual rainfall between 50 and 100 mm are found adjacent to this section, the Orange River Valley, and parts of the Knersvlakte and Doring–Tanqua Karoo. Rainfall is usually cyclonic and its kinetic energy is lower for the biome as a whole compared to the other biomes (Schulze 1980). Hailstorms are rare and the average number of days with thunder is usually much less than about 15 per annum. The density of lightning flashes to ground are usually

less than one per annum (Kroninger, quoted Edwards 1984). Fog is common along the coastal plain. The biome has the shortest summers with a duration of less than  $6\frac{1}{2}$  months (198 days) (Schulze 1965). The length of the period in which frost can occur is considerably less than 90 days and frost is seldom severe. Many areas have no frost. Incoming radiation in summer is greater than 270 to  $280 \text{ J m}^{-2} \text{ day}^{-1}$  which is higher than that for the other biomes according to Schulze & McGee (1978). Summer temperature maxima can be very high. Absolute values of greater than  $44^\circ\text{C}$  have been recorded. Desiccating berg winds also occur.

The vegetation of the biome is dominated by chamaephytes which are often succulent. Therophytes and geophytes can also be common but only attain (co)dominance in areas of sub-biomic proportion. Mass flowering displays of certain therophytes (usually of Asteraceae) especially in Namaqualand in spring, are often associated with degraded, overgrazed lands. Despite the sometimes large number of therophyte and geophyte species such as in Namaqualand, the 'physiognomy of the vegetation has a decided chamaephytic character' (Rösch, quoted Van Rooyen *et al.* 1979). Graminoid hemicryptophytes are generally rare (Rycroft 1968) but can be important on limited areas of sandy substrate. Phanerophytes are rare but include the well known succulent *Aloe dichotoma* in the north. The difference in life form dominance between Succulent Karoo Biome and Nama-Karoo Biome is aptly encapsulated in the vegetation unit terms used by Giess & Tinley (1968) for the corresponding areas in South West Africa/Namibia, namely, 'Karoo Succulent Steppe' and 'Karoo Shrub and Grass' respectively.

The biome is very rich in succulent plant species belonging mainly to the Mesembryanthemaceae and Crassulaceae but also to many other plant families. Many species are endemics or near endemics (Werger 1978b). Species diversity is high for an arid region and there are a considerable number of rare and endangered species in the biome (Hall *et al.* 1980). The high succulent plant species diversity of this biome is unparalleled elsewhere in the world.

Seeing that most succulents have a CAM photosynthetic pathway, this pathway is important in much of the Succulent Karoo Biome (Werger & Ellis 1981). Most of the species that constitute the rather unimportant grass flora of the biome have the  $C_3$  photosynthetic pathway in contrast to the  $C_4$  grasses of, for example, the Nama-Karoo Biome (Vogel *et al.* 1978). However,  $C_3$  grass species are in a minority in the winter rainfall area of South West Africa/Namibia although this area still has the highest proportion of  $C_3$  grass species in the territory (Ellis *et al.* 1980). An interesting distinction is also indicated between Succulent Karoo Biome and Nama-Karoo Biome by Werger & Ellis (1981) in terms of malic and aspartic acid forming groups of  $C_4$  plants. In contrast to the Nama-Karoo Biome, the (few)  $C_4$  grass species of the Succulent Karoo Biome all appear to be aspartate formers. The general preponderance of  $C_3$  over

$C_4$  grass species in the Succulent Karoo Biome may relate to the ability of especially the  $C_3$  grass species to grow in the cooler months (see Pierce 1984) although the general growth rates of plants decreases to a very low level during the winter months despite favourable moisture conditions (Van Rooyen *et al.* 1979).

Adaptation to arid conditions through drought avoidance by storage of water is important for the succulents of this biome. Most of the other chamaephytes adapt through drought tolerance. Drought evading xerophytes include the therophytes (evasion in time) and many geophytes (evasion of the desiccating above-ground environment).

Any successional changes in vegetation in the Succulent Karoo Biome are detected with difficulty owing to the very slow rates of natural vegetation development or change in this biome. Roux & Vorster (1983), while acknowledging the 'relative paucity of factual data', postulate five phases of change in the vegetation of Karoo. These correspond to five seral phases of desertification ranging from initial high cover of perennial grass to virtual absence thereof in phase 5. They indicate that it is the large proportion of the Succulent Karoo Biome that is in this final desertified phase. However, the clear climatic distinction of this biome from the Nama-Karoo Biome (Fig. 10) makes it necessary to reappraise the postulated dominance or codominance of perennial grass\* in the Succulent Karoo Biome. The present work supports Roberts's (1981) contention that 'permanent "grassiness" has apparently never been an inherent characteristic of the western regions of the karoo' and that, for example, the very largely grassless Little Karoo 'has probably been in this state for as long as the arid climate has prevailed in the area'. It is noteworthy that various agricultural plant seeding programmes have had far greater success with introducing chamaephyte species than perennial graminoid hemicryptophyte species to this biome. Perennial grass plant cover in an area protected from grazing for 50 years in the Robertson Karoo has increased (P.A.B. Van Breda pers. comm.) but is still very low compared to the cover of the chamaephytes. In an area of Namaqualand, Van Rooyen & Grobbelaar (1982) found no identifiable grass species in the seed bank of the area. Acocks (1975) who was strongly influenced by successional theory, labeled many vegetation areas of South Africa, including karoo, as 'false'. These areas are thought to be degraded and to have had a greater perennial grass cover (except for his false grassveld types). It is interesting to note that even Acocks (1975) indicates virtually no areas as 'false' in the area of the Succulent Karoo Biome.

Above-ground plant production in the biome is mostly between 200 and  $1\,000 \text{ kg ha}^{-1} \text{ a}^{-1}$  and can attain  $2\,000 \text{ kg ha}^{-1} \text{ a}^{-1}$  only in the wettest parts of the biome. Above-ground plant biomass (dry mass) varies from about 0,5 to 7 metric t ha<sup>-1</sup>. The low fuel load and high frequency

\* The low level of this component is essentially diagnostic for the Succulent Karoo Biome.

of non-flammable succulent plants (Edwards 1984) results in virtual exclusion of fire in the biome. Plants of the biome appear to be sensitive to fire and effects are long-lasting. In an area of the Robertson Karoo, close to the upper rainfall limit of the biome, a forced fire was applied using artificial ground fuel which changed the chamaephyte species dominance which has persisted for almost 50 years (Olivier 1966; P.A.B. van Breda pers. comm.).

Very few zoological data are available for the Succulent Karoo Biome. Although there are some similarities with the fauna of the Nama-Karoo Biome, certain insect groups in the Succulent Karoo Biome show closer affinities with the Fynbos Biome than with the Nama-Karoo Biome (C.H. Scholtz pers. comm.). This, incidentally, would support a 'winter rainfall biome' proposed on altogether different grounds (Bayer 1984). Certain bee species are associated with the Succulent Karoo Biome (V. Whitehead pers. comm.).

Only 0,47% of the area of the Succulent Karoo Biome in South Africa is conserved and the biome has the lowest conservation status in southern Africa. There are currently no areas of minimum biome dimension conserved. This does not take into account restricted diamond areas of the northern part of the biome where the conservation status is unclear. Since the biome has a high floristic diversity and species endemism and is globally unique in its succulent plant species diversity, the low percentage area formally conserved requires review and conservation action. The planned Richtersveld National Park will assist in rectifying the conservation imbalance but will not provide adequate conservational coverage of the biome.

The spread of alien invasive plant species in the biome is mainly limited to relatively minor incursions along certain river courses, for example, *Nicotiana glauca*, and along the west coast where, for example, *Acacia cyclops*, occurs. Some areas of natural vegetation are being overseeded with alien plant species such as *Atriplex nummularia* from Australia in an attempt to raise the carrying capacity for grazing stock.

The Succulent Karoo Biome may be divided in two major natural divisions based on moisture availability:

(1) The arid succulent karoo plains include most of the flat, low altitude basins and the Namaqualand coastal plain [almost equivalent to Acocks (1975), Succulent Karoo Veld Type No. 31] and the South West African/Namibian part of the biome. The vegetation usually contains a higher proportion of succulent elements and the vegetation height and canopy cover is generally lower than in the other division. Patches of arid grassland on sand are limited to this division.

(2) The less arid succulent karoo brokenlands include much of the more broken veld with rolling hills, for example, in Namaqualand, Little Karoo and Robertson Karoo. The vegetation usually contains an important but lower proportion of succulent elements and the vegetation height and canopy cover is generally higher than in the arid succulent karoo division. Hemicryptophytic graminoids are rare. The border between these two

divisions lies between the 115 and 125 mm isohyets. The division of the biome corresponds roughly to Adamson's (1938) essential division of 'Succulent Bush' into 'Low Succulent Bush' and 'Tall Succulent Bush'.

Very little research has been carried out on the Succulent Karoo Biome. In common with the Nama-Karoo Biome, it has no university within its borders but unlike the Nama-Karoo Biome it does not contain an active agricultural research centre similar to that at Middelburg, Cape, and is very distant from this centre. Much of the research that has been done has been mounted from centres within the adjacent Fynbos Biome area. Apart from limited work done by agricultural bodies, nature conservation and botanical gardens in the biome, sporadic local research has been supplemented by occasional overseas researchers (for example, Eller *et al.* 1983) who recognize the uniqueness of the vegetation and flora of the Succulent Karoo Biome.

Carrying capacity for domestic stock, mostly sheep but replaced with goats in some areas, is generally lower than that of much of the Nama-Karoo Biome (Rutherford 1981). Grazing capacities are so low (as low as, for example, 9 ha ssu<sup>-1</sup> — Baard 1978) that grazing is often obtained from cultivated fields and is only supplemented from natural vegetation except in years of adequate rainfall. In the Little Karoo several hundred farmers farm with ostriches exotic to the area. Cultivation is usually limited to strips alongside water courses. In some areas adjacent to the Fynbos Biome, wine grapes and other crops are cultivated with water from catchments in the Fynbos Biome.

Urbanization within the biome is limited to two medium-sized towns (Worcester and Oudtshoorn) and various smaller centres. Within the arid succulent karoo division even small centres are limited to the more mesic periphery or to the coast. Current tourism includes tours of spring wild flower displays, especially in Namaqualand, and ostrich show farms in parts of the Little Karoo. The rugged topography of the Richtersveld and parts of the western escarpment has some tourism potential. In the southern portions, tourism within the biome tends to be offset by greater scenic and other attractions of the nearby Fynbos Biome.

The biome is rich in mineral deposits, mainly in the northern parts. Medium and larger mineral deposits in the biome are (in approximate descending order of size): copper, uranium, diamonds, rare earths, kaolin, beryllium, tungsten, phosphate, tantalum-niobium, zirconium, dolomite, molybdenum, lead, zinc, titanium, lithium, bismuth, fluorspar, mica, manganese, limestone, thorium, attapulgite, sepiolite, kieselguhr, gypsum and sillimanite.

The biome has been subjected to grazing first by stock of nomadic tribes and was the first biome in southern Africa to be intensively grazed by European settlers' stock from early in the 18th century. Although much soil of the biome has been lost through erosion related to overgrazing, it is difficult to find evidence to support the notion that excessive soil loss has occurred in every part of this biome in historical time.

#### 4.9 Comparisons

Three of the biomes determined by this study have already been accepted by more than half the representative sources cited before (Fig. 4; Table 1), as major natural biotic divisions. These are the Fynbos, Grassland and Forest Biomes. Most of these sources have not differentiated their arid zone into the determined Nama-Karoo, Succulent Karoo and Desert Biomes. Just over half the sources, on the other hand, have split the determined Savanna Biome into a number of often mutually conflicting units (Table 1).

Although the determined biomes are unique as a set, each individual biome has been proposed by several of the above-mentioned sources.

The biomes recognized for South Africa in this study agree best, in both concept and area, with those of Adamson (1938). All the biomes correspond except for his arid zone area ('semi-desert') which he divided into arid bush and succulent bush which correspond with the Nama-Karoo and Succulent Karoo Biomes respectively. Similarly the major vegetation units of Acocks (1953, 1975) on Map No. 2 — Vegetation in AD 1950, correspond to biomes here recognized, except for his division of grassland and the status given to desert patches. Many of the anomalous groupings in the veld type map of Acocks (1975), such as his placing of Valley Bushveld under Karoo and Karroid types, he groups correctly on his Map No. 2. The veld types would have been ecologically more meaningful had he grouped them according to his Map No. 2. Acocks himself states that Map No. 2 is 'merely a simplified version of the veld type map' and foresees that in years to come Map No. 2 'will be the basis for further comparisons'.

In contrast to Adamson (1938) the other four sources who also limit their classifications to the five most frequently used units (Section 1.5), fail to recognize any units corresponding to the Nama-Karoo and Succulent Karoo Biomes.

Many other sources tend to excessively subdivide areas with which they are more familiar or they lump major units in less well known areas. The main tendency to lump major units of the arid zone possibly reflects the low level of urbanization (see Sections 4.2; 4.6 and 4.8) which is usually associated with a low research effort. The bias in such sources has been widely recognized to reflect their knowledge of any given region and their main research interests (Leith & Van der Maarel 1976). With the exception of Acocks (1975, veld type map, not Map No. 2) all sources with more than a third of their units in the unique natural biotic divisions (Table 1, Group IV) were not native to the region.

Jacobsen's (1983) five major vegetation groupings for southern Africa include various anomalies such as grouping the Fynbos Biome, most of the Nama-Karoo Biome and parts of the Savanna Biome into a single major unit.

The set of major vegetation divisions of Rycroft (1968) is limited to the area of the Cape Province but

nevertheless corresponds with the determined biomes except for the grouping of savanna and grassland, and the inclusion of desert in the Province.

Denys's (1980) floristically based objective method of determining phytogeographical divisions for southern Africa suffers from an inadequate data base and an excessively coarse sample grid and results in a coverage of less than half the area and in anomalous units in terms of the present study.

The major recent work of White (1983) deserves detailed attention to illustrate some of the problems often encountered in delimiting major natural units. White's (1983) sixteen major physiognomic divisions (= formations of regional extent) are the only defined structural units and are obtained by *a posteriori*, informal, subjective classification process. Although White objects to Raunkiaer's system of life form classes, his system also relies heavily on height classes. No distinction is made for heights below 2 m and most attention is given to dividing the range of 2 to 10 m. Raunkiaer's major subdivisions, in contrast, place most emphasis on dividing the range below 2 m height which is more significant in terms of various microclimatic gradients, fire effects and utilization by most ungulates. The often extremely variable canopy cover criterion, used by White (1983), is inappropriate to the mapping scale, because this often results in an inordinately wide scatter of the mapping unit. It would appear that the variable cover coupled with considerable spatial variability in the heights used, has precluded the author from mapping many of his defined structural units and has forced him to employ conglomerative structural units apart from transitional and other units. Some of the 'major physiognomic divisions', for example, the Afro-alpine vegetation, are based primarily on non-physiognomic criteria. The structural unit definitions are usually based on a single vegetation stratum, which makes application difficult in multi-stratal vegetation. Furthermore, some of the major physiognomic divisions are not defined to be mutually exclusive, which leads to difficulties in application that are avoidable when using structural schemes, such as that of Edwards (1983).

The 'concordance of chorology and physiognomy' (White 1983) is scale-dependent (see Section 6) but even at the appropriately small scale, the choice of physiognomic parameters would make close concordance unlikely. The phytocoria (centres of endemism) are defined as areas where at least 1 000 plant species are endemic and these constitute at least 50% of the total number of species in the unit. This definition, although arbitrary, is welcome compared to past classifications in which phytocoria have usually been very vaguely defined. The largest phytocorion mapped south of 22°S is not a centre of endemism but a Regional Transition Zone. Other units of phytocorial rank include regional mosaics and non-contiguous 'archipelago'-like areas. The largest proportion of this area (that is, transitions and mosaics) does not conform to White's (1983) phytocorial definition. This detracts from the usefulness of the phytocorial

definitions as applied in southern Africa. Objectivity would be enhanced if phytocoenoses were differentiated using appropriate multivariate techniques.

There is little correspondence between the classes of the well known Köppen (Schulze & McGee 1978) or Thornthwaite (Schulze 1958; Poynton 1971; Schulze & McGee 1978) climatic classifications of southern Africa and the determined biomes. Only the Cwb climatic unit of the Köppen system approximates the area of a biome, namely, the Grassland Biome. Thus, even the Köppen system 'still leaves much to be desired in its attempts to relate vegetation to broad climatic parameter values' (Schulze & McGee 1978). Jackson's (1951) attempt to improve the deficiencies of the Köppen and Thornthwaite systems is based on no fixed criteria and results in climatic units which do not correlate with any determined biome. From these and other such climatic classifications of southern Africa it appears that these serve no purpose in differentiating vegetation at biome scale. Failure to incorporate and combine climatic parameters directly relevant to vegetation have resulted in a lack of correlation with vegetation. Because existing climatic classifications do not correspond to biomes of southern Africa, these were not employed in the present study and the more relevant climatic system described before (Section 2.3) was devised to make use of the available data.

#### 4.10 Concluding remarks

From a consideration of the distribution of the major soil groups (MacVicar 1973) and geological units, it is clear that biomes cannot be delimited on the basis of these and even less on the basis of finer subdivisions of soil or geology. Not one of the major soil groups or geological units of larger area is associated exclusively with a particular biome and even with subdivisions, associations with biomes are limited in number and generally occupy less than 10% of the biome concerned. An exception is the Table Mountain Group which occupies a larger percentage

in the Fynbos Biome. The problem of delimiting biomes on the basis of soils or geology, is exemplified by the Savanna Biome where all the major soil groups and most of the geological units are present. It is possible that the tenuous link between some soil groups and biomes could be strengthened if parameters more relevant to vegetation and climate were used to classify soils. The links between geological units and biomes are considerably weaker than with soils. This is expected, where pedogenesis, in contrast to lithogenesis, is climate and vegetation dependent. Pedogenesis does not depend only on climate and vegetation but on several other important factors including, geology, topography and past climatic patterns, so that strong links between soils and biomes remain unlikely.

Of all the classifications of major biotic areas of southern Africa, the most similar classification to that of the present study is that of Adamson in 1938. Despite numerous publications, the erratic progress in this field during the intervening period suggests poor observance of scientific principles and lack of research direction and purpose. The lack of appreciation of hierarchy theory is clearly evident in some works in this field where, for example, 'biomes' are purported to fall within 'biomes'.

Popular classifications that are based purely on climate, such as those of Köppen and Thornthwaite, have been shown to be of virtually no use in correlating with major vegetation units at biome scale. Any classification of natural systems that ignores vegetation (the primary producer component) is likely to be irrelevant to functioning of the ecological system.

There are few available distribution data for most zoological taxa in southern Africa. In addition, zoologists have tended to specialize according to taxonomic groups rather than ecologically functional groups. This has resulted in a lack of an ecologically based zoological synthesis which has limited comparisons at biome scale to pitifully few groups.

The principal subdivisions of the biomes in relation to mean annual rainfall are summarized in Fig. 20. Areas where subdivisions overlap in terms of mean annual

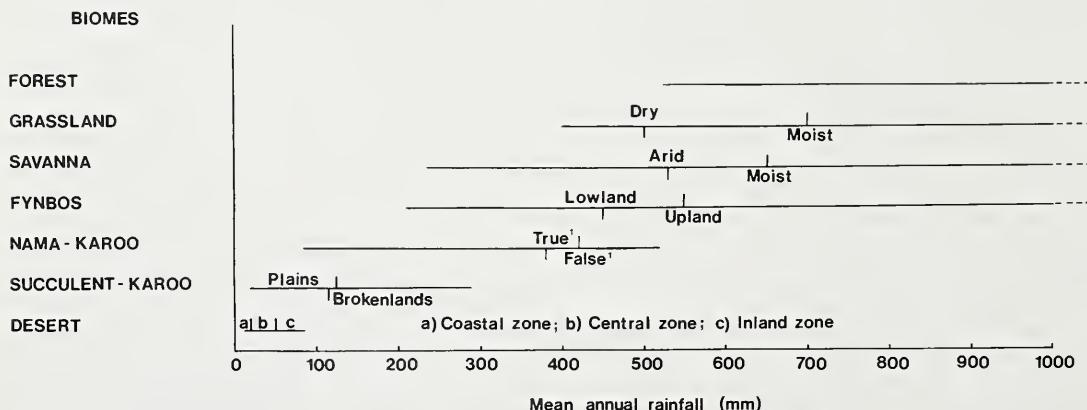


FIG. 20.—The relationship between mean annual rainfall up to 1 000 mm and biomes with their principal subdivisions. Areas of overlap indicate where additional factors can be significant in delimiting these subdivisions. Area limitations preclude equivalent levels of subdivision in the Forest Biome. 'True and False refer to correspondence and non-correspondence between climate and dominant life forms, respectively.

rainfall indicate the domain where additional factors can be significant in delimiting the subdivisions. The biological effect of the same climatic factor of a certain strength can be very different if other factors of the whole complex are changed (Boyko 1962). The area of overlap increases with increasing minimum rainfall for each biome.

Increased plant survival is generally associated with decreasing height of the renewal buds, that is, from chamaephytes through to geophytes (Chapman & Crow 1981) (Fig. 1). However, many phanerophytes of the Savanna Biome are able to survive fire in strong contrast to many in the Fynbos Biome, which die.



## 5 Ecological and environmental relationships of dominant life forms

### 5.1 Phanerophytes

Rainfall seasonality is not limiting to the dominance of phanerophytes. The lower climatic limit for dominance at biome scale is a function of the summer aridity index (SAI) and rainfall seasonality. The absolute maximum SAI for dominance of phanerophytes is about 6,0 in areas with the greatest proportion of rainfall in the winter half-year. In areas with the greatest proportion of rainfall in the summer half-year, the maximum SAI decreases to about 3,75. The lowest limit for dominance of phanerophytes therefore varies from about 20 to 190 mm in the four hottest months of the year. The lower limits for dominance also approximate a mean annual rainfall of 235 mm but a lower mean annual rainfall can support Succulent Mountain Scrub (Spekboomveld). Succulent Mountain Scrub is also the savanna type that is subjected to the highest degree of summer drought and this may relate to the water storage capability of the dominant phanerophyte (*Portulacaria afra*) of this veld type. Phanerophytes of the Fynbos Biome can experience an even greater degree of summer drought, but despite sclerophyll, require a mean annual rainfall higher than 235 mm. Only in the form of parts of the marginally phanerophytic Mountain Renosterbosveld can they tolerate rainfall as low as about 235 mm per year. The phanerophytic component in the summer rainfall area does not extend into areas where mean annual rainfall is as low as 235 mm and temperature minima are sufficiently low.

The seedling is the most vulnerable stage in the life cycle of a phanerophyte in its competition for resources and susceptibility to frost. Phanerophytic dominance can occur over almost the entire range of minimum temperature data available in southern Africa except for parts of areas with monthly mean screen minima below about -1°C. In areas with mean monthly minima below -1°C, phanerophytic dominance is affected by the amount of moisture received. Thus, phanerophytic dominance is excluded from these cooler areas with higher summer rainfall but not necessarily from the cooler areas with lower summer rainfall. In this way, phanerophytic dominance can occur in the cold arid northern Cape Province of South Africa but is not

encountered in the cold and relatively moist grasslands. This pattern may be attributed to an increased cold hardening effect linked to the reduced availability of water in the growing season in the cold arid savannas. This possible adaptive resistance to low-temperature injury in phanerophytes and their seedlings is supported by findings of increased hardening by withholding water prior to occurrence of frosts in certain orchards (Daubenmire 1974). Perched gleys may result in excessively wet soils in the growing season and thereby prevent woody seedlings from developing on the South African highveld (Tinley 1977), however, areas of gleys and perched gleys are very limited in this region (J. Schoeman pers. comm.). It appears that the frost factor, which is regarded as 'additional' by Tinley (1977), should rather be considered a major determinant for exclusion of most trees in the highveld area. Frost in montane regions does not occur in forest patches within these regions (Adamson 1938).

The lower limit for occurrence of unidominant stands of phanerophytes (forests) corresponds, on average, to a mean annual rainfall of 625 mm. This is influenced by the temperature of the rainfall season so that the lower limit decreases to about 525 mm in areas with strong winter rainfall and increases to about 725 mm in areas with strong summer rainfall. In areas close to these limits, forests are usually limited to relatively specialized habitats, for example, landscape incision-breaks. As rainfall increases, the frequency of occurrence of forests increases but the paucity of high rainfall areas in southern Africa and the above-mentioned effects of minimum temperature preclude the development of extensive forest. The relative uniformity of life form subdivisions (for example, evergreens) in forest and the apparently simple dependence on rainfall is not reflected at the lower limits of phanerophytic dominance where the wide range of dominant life form subdivisions, for example sclerophylls, succulents and deciduous plants, are found.

The limitation of phanerophytic dominance to the wetter areas may relate to this life form generally having the largest transpiring surface area compared to the other life forms (Box 1981b). Even where chamaephytes are closely packed, the greater canopy depth usually found in phanerophytes with the same vertically projected

cover per unit area can still result in a larger transpiring surface area. It follows that phanerophytes usually require more water than the other major life forms. Indeed, the height of certain phanerophytic species has been found to decrease to chamaephytic height along a gradient of decreasing soil water potential values (Balding & Cunningham 1974). Orshan *et al.* (undated) state that in South Africa a decrease in the percentage of phanerophytes is primarily due to water stress. Plant height is generally positively related to increased water use (Rosenberg *et al.* 1983). The generally lower height of phanerophytes of the Fynbos Biome compared to that of the Savanna Biome, may be related to summer desiccation, exacerbated by for example, persisting winds. The taller the plant, the more subject it is to desiccation (Daubenmire 1974). Phanerophytic height limitation in fynbos, in contrast to savanna, may also be associated, *inter alia*, with the inability of many fynbos phanerophytic obligate seeders to survive fire under conditions of a frequently recurring, often uniquely intense fire (Moll *et al.* 1980). Also, within savanna areas where low phanerophytes dominate, for example in Succulent Mountain Scrub and parts of the Kalahari Thornveld, high Summer Aridity Index values usually occur.

## 5.2 Chamaephytes

As with the phanerophytes, rainfall seasonality is not limiting to the dominance of chamaephytes. The lower climatic limit for dominance at biome scale is also a function of the SAI and rainfall seasonality. But the absolute maximum SAI for dominance of chamaephytes is about 7,5 in areas with the greatest proportion of rainfall in the winter half-year. In areas with the greatest proportion of rainfall in the summer half-year, the maximum SAI decreases to about 4,6. The lowest limit for dominance of chamaephytes, therefore, varies from about 5 to 80 mm in the four hottest months of the year. In areas with a low percentage winter rainfall, the upper SAI limit for chamaephytic dominance approximates a constant mean annual rainfall value, but in areas of increasing winter rainfall it coincides with greatly decreasing mean annual rainfall values. Perennial vegetation can exist in these extremely arid conditions of the latter areas because of: 1, the strong tendency of chamaephytes toward succulence; 2, the possibly increasing effectiveness of rainfall due to reduced winter rain evaporation; and 3, selective water supplementation and reduced evapo-transpiration through regular coastal fog. The lower SAI limit for dominance of succulent chamaephytes is about 4,9, that is, not more than 60 mm in the four hottest months. Succulent plants are well adapted to this hot, dry summer area because of their water storing ability enabling them to bridge the summer drought and exhibit the commonly encountered CAM photosynthetic pathway with increased water use efficiency. However, owing to very low stomatal conductance at night, it is unlikely that CO<sub>2</sub> fixation in the dark can confer any

competitive advantage in terms of productivity (Osmond *et al.* 1982). In the limited areas also with high SAI values but with lower minimum temperatures, succulent chamaephytes cease to dominate. Some authors (Werger & Ellis 1981) have suggested that the frequent occurrence of CAM succulents in the south-western subcontinent is related to 'low but sufficient and perhaps regular moisture supply'. A fairly regular supply of moisture may be required outside the four hottest months but the above evidence does not support the notion that dominance of succulents requires a fairly regular supply of moisture throughout the year. Possible effective water additions through fog during the summer months are limited to the narrow coastal belt and do not occur throughout the Succulent-Karoo Biome. The association of succulence with greater mean seasonal aridity is, however, not incompatible with association of succulence with reduced variability in *annual* rainfall (Ellenberg 1981) although the latter association is very approximate in southern Africa.

In the summer rainfall area, the lower SAI limit for chamaephytic dominance is about 3,8 but can extend to as low as 3,2 in the cooler and wetter areas previously dominated by hemicryptophytes alone. These areas correspond to the well-documented (for example, Acocks 1975) management-induced karoo invasion of grasslands. In the winter rainfall area, chamaephytic dominance can extend to much lower levels of SAI than in the summer rainfall areas. The generally lower and smaller phanerophytes with reduced resource requirements and competitive effectiveness in the former area, may permit the dominance of chamaephytes together with phanerophytes. In areas with dominance of larger phanerophytes with increased resource requirements and competitive effectiveness, the occurrence of chamaephytes is limited. In many other systems throughout the world, codominance of phanerophytes and chamaephytes seems to be the exception rather than the rule. In contrast to phanerophytes, chamaephytic dominance occurs over the full range of minimum temperatures in the subcontinent.

## 5.3 Hemicryptophytes

Most dominant hemicryptophytes in the subcontinent belong to the Poaceae and grow most effectively in the warm season where they require adequate levels of water and radiation. Dominance of these forms can occur up to an SAI limit of between 4,9 and 5,2, that is, not less than 45 to 60 mm rain in the four hottest months. In areas with a high proportion of rain in winter, hemicryptophytic dominance can occur up to an SAI limit of about 6,0, that is, as low as about 20 mm rain in the four hottest months. However, these hemicryptophytes differ in that they are mainly hardy, aphyllous members of the Restionaceae. At higher rainfall levels (for example, mean annual rainfall > 400 mm), dominance of restioid hemicryptophytes in the winter rainfall areas tends to be replaced by graminoid hemicryptophytes with increasing proportion of summer rainfall, particularly above 60%.

Several restioid plant species differ from grasses in that they tolerate very low summer xylem water potentials, yet remain evergreen (Miller 1982; Moll & Sommerville 1985). As with chamaephytes, hemicryptophytic dominance occurs over the full range of minimum temperatures in the subcontinent. Even though distributional data for geophytes in southern Africa are scanty, it appears that the environmental and ecological relationships of geophytes do not differ substantially from those of hemicryptophytes. In his treatment of life forms in relation to environment, Schulze, E.D. (1982) also groups geophytes with hemicryptophytes as perennial herbaceous plants. Similarly Frankenberg (1978) groups these two life forms together as does Raunkiaer who terms the combination the Hypogeous class (Du Rietz 1931).

#### 5.4 Therophytes

Water stress in therophytes is overcome by drought evasion in the form of seed. Therophytic dominance occurs in areas with lowest rainfall and greatest degree of summer drought where dominance of perennial plants is excluded. Therophytes can also be common in slightly higher rainfall areas where succulent and/or woody chamaephytes are dominant but therophytes do not satisfy their dominance criterion in these areas. Reduction in plant cover through disturbance can result in local therophytic dominance in any biome but is more prevalent in the drier areas. The minimum rainfall required for germination of therophytes has been reported to be an individual shower of 15 mm (Tevis 1958) and seeds are thus prevented from germinating after trivial showers (Smith 1974). In the Namib Desert, Seely (1978a) has demonstrated that 17 mm rain is sufficient for germination and harvestable growth of therophytes. Although regular fog is used by certain specialized perennial desert plant species (Seely 1978b), it appears that fog is inadequate for growth of therophytes (Robinson 1976). It should be noted that fog water is inadequate for successful

germination of the perennial plant *Stipagrostis sabulicola* and that at least 20 mm of rain is required (Louw & Seely 1980). For areas with mean annual rainfall less than these minimum values for germination and for harvestable growth, therophytic dominance can still occur when these minimum values are attained. Despite the relative ease with which therophytes become established, the plants are particularly susceptible to adverse environmental conditions for the remainder of their lifespan. In southern Africa, the area with therophytic dominance does not have negative mean lowest minimum temperatures for the coldest month.

#### 5.5 Concluding remarks

Despite the controversy surrounding the occurrence of grasslands in various parts of the world (Coupland 1979), the present study provides a coherent explanation for these areas in southern Africa.

The similarity of geophytes and hemicryptophytes, in terms of many of their environmental relations, is confirmed by the world-wide observations that no climate correlates specifically with geophytes (or cryptophytes) (Cain 1950; Fekete & Szukla-Lacza 1971). This substantiates the finding that the geophyte life form is not of equivalent rank to that of the other four main life forms.

There is a paradoxical relationship between the strengths and weaknesses of plants of a given life form. Despite the association of therophytes under the most adverse environmental conditions through to phanerophytes under the most favourable environmental conditions (owing to their different resource requirements), the order of life forms is reversed in terms of the susceptibility of the plant to adverse conditions during its period of active growth. Established phanerophytes can withstand the greatest range of such adverse conditions whereas therophytes can withstand only the least adverse conditions during active growth.



## 6 Rationalization of relations between mapping scale, vegetation structure and floristic community

Factors influencing comparison and integration of different vegetation maps include detail and cartographic accuracy. The amount of detail which can be shown on a map is scale-dependent. However, this scale-dependency refers to working scale or associated sampling scale and not final publication scale because the latter can be considerably reduced or enlarged and still retain the detail of the original working or sampling scale. Typographically, it is very difficult to represent gradations and very often limits are drawn with an accuracy which does not exist in nature (UNESCO 1973). Users of vegetation maps seldom require a linear precision of less than a millimetre which is often commensurate with manual cartographic accuracy. Lines demarcating units on a vegetation map may, therefore, lie as much as a millimetre in either direction from that indicated, irrespective of scale. This level of precision determines the maximum detail of the publication scale and therefore determines the maximum detail appropriate to the working scale. At the working scale, the area under study is subdivided by lines separating stratified units which contain the potential sample sites. Sample sites at working scale, should: 1, not be closer than 1 mm to a stratified unit's border; and 2, not be closer than 2 mm to another sample site. It follows from condition 1 that the real width of an unmappable ecotone or transition is scale-dependent. From these geometric considerations, a grid size of  $4 \times 4$  mm should be used at any given working scale (Fig. 22) as a map overlay for selecting stratified random or systematic sample sites. The relationship of working scale to the smallest mappable unit area (SMUA) is derived from the distance from sampling unit area to stratified unit border and is given in Fig. 21:

$$y = e^{(-12.67 - 2 \ln x)}$$

where  $y = \text{SMUA}$  in  $\text{m}^2$ , and  $x = \text{scale}$ , as a representative fraction. The minimum sampling distance from a stratified unit border in the field (MSDB) is therefore, expressed as:

$$\text{MSDB} = \sqrt{\frac{y}{\pi}}$$

where MSDB is in metres. The shortest cross distance of

a mappable unit (SCD) in the field is expressed by:

$$\text{SCD} = \sqrt{\frac{4y}{\pi}}$$

where SCD is in metres.

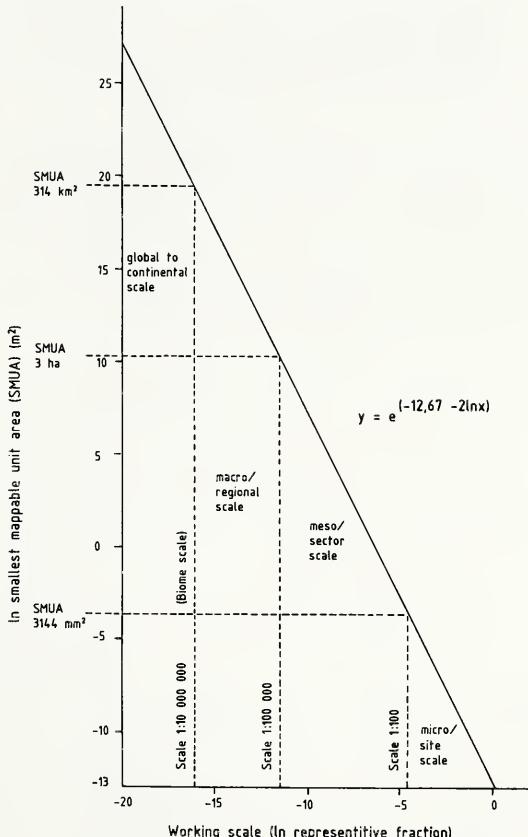


FIG. 21.—The relationship between sampling scale and smallest mappable unit area (SMUA) where  $y = \text{SMUA}$  in  $\text{m}^2$  and  $x$  is the denominator of the sampling scale expressed as a representative fraction.

Examples of SMUA, MSDB and MSA for selected scales are given in Table 9. The SMUA is the smallest unit that can be depicted on a map, commensurate with manual cartographic accuracy and corresponds to the

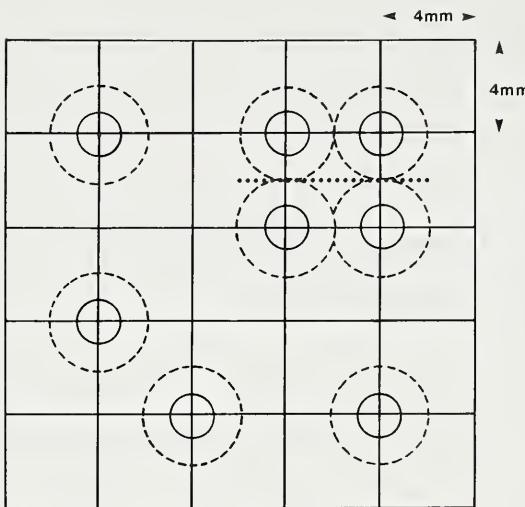


FIG. 22.— $4 \times 4$  mm grid for map overlay to determine possible sample sites. Solid circles represent the smallest mappable unit areas (SMUA); the dotted line represents a border; the diameter of the SMUA = shortest cross distance (SCD); and the radii from solid circles to broken circles = the minimum sampling distances from borders (MSDB).

smallest area in which more than one sample set would be redundant for mapping purposes. At biome scale it is impracticable for sample size to be that of the SMUA ( $314 \text{ km}^2$ ; Fig. 21). Even panoramic photographs of the vegetation at this scale can be misleading because only a small fraction of the SMUA is normally obtained. For this reason photographs of biomes could be misleading and have not been included in this work.

Floristic communities vary both in area and rank. Because rank can be assessed only after classification, area is relevant during sampling. To differentiate a community adequately, a sample set should be floristically representative of the SMUA and contain most, if not all, of the species in the SMUA. The sample set, therefore, will be less than or equal to the area of the SMUA. Taxa representing communities too small to be differentiated at a given working scale, will be included in larger

communities. Appropriate working scale is a function of area and number of sample sets (which is usually governed by time).

The maximum number of sample sets that can be included in a given area with the appropriate spacing is:

$$N = \frac{10^6 A}{4 \text{ SMUA}}$$

where N is the number of sample sets and A is the area in  $\text{km}^2$ . Analysis of current and completed vegetation sampling data indicates that N can vary from 0.5% to 4%, of the maximum number of sample sets possible. The value in most cases approximates 2%. Sampling intensity (N) where the area has not been stratified prior to sampling is therefore

$$N = \frac{5000A}{\text{SMUA}} \quad \text{or}$$

$$N = e^{-\frac{1}{12,67 - 2 \ln x}} \times 5000A$$

area (A) is:

$$A = e^{(-12,67 - 2 \ln x)} \times \frac{N}{5000}$$

and scale as a representative fraction (x) is:

$$x = e^{\frac{\ln \frac{5000A}{N} + 12,67}{-2}}$$

The heterogeneity of vegetation can be taken into account by stratification of the vegetation prior to sampling. This can influence the number of sample sets required. The minimum area (MA) which can be stratified at a given scale is given by:

$$MA = 4 \cdot \text{SMUA} \cdot n \text{ in } \text{m}^2$$

where n is the maximum number of sample sets required for community differentiation. The value of n can be in the range of 8 to 20 according to stratification unit area

TABLE 9.—Examples of smallest mappable unit area (SMUA) minimum sampling distance from border (MSDB) and shortest cross distance (SCD) for selected scales

Scale	SMUA $\text{m}^2$	SMUA to nearest	MSDB*	SCD
1:1	0,0000031	3 $\text{mm}^2$	1 mm	2 mm
1:10	0,0003144	314 $\text{mm}^2$	10 mm	20 mm
1:100	0,0314404	31440 $\text{mm}^2$	100 mm	200 mm
1:1 000	3,1440461	3 $\text{m}^2$	1 m	2 m
1:10 000	314,40461	314 $\text{m}^2$	10 m	20 m
1:50 000	7860,1154	1 ha	50 m	100 m
1:100 000	31440,461	3 ha	100 m	200 m
1:250 000	196502,88	20 ha	250 m	500 m
1:500 000	786011,54	78 ha	500 m	1 km
1:1 000 000	3144046,1	314 ha	1 km	2 km
1:10 000 000	314404616,5	314 $\text{km}^2$	10 km	20 km
1:50 000 000	7860115412,0	7860 $\text{km}^2$	50 km	100 km

\* 1 mm on map = MSDB value on ground at given scale.

and provides for subdivision of a stratified unit into different floristic communities. The total number of sample sets ( $N$ ) can then be adjusted accordingly to account for vegetation heterogeneity.

Even if sampling and mapping were uniform, horizontal integration of floristic maps would still be difficult because of the different ranks or the hierarchical nature of floristic communities which would necessitate knowing all the smallest floristic units, to ensure that a particular unit is not merely an outlier of a larger unit. A main objective of a vegetation classification should be prediction of vegetation classes from correlation with environmental factors. The increasing complexity of vegetation/environmental relationships with increasing scale is illustrated in Fig. 23. This complexity exacerbates the difficulties of horizontal integration of different large scale floristic maps and difficulties of grouping floristic units into smaller scale units. Changes over time are generally more rapid at large scale than at small scale. A divisive mapping strategy where the vegetation is classified into the largest possible units and is subsequently divided overcomes these problems of integrating vegetation units by having a small determinate number of reference points for ranking and maintains perspective.

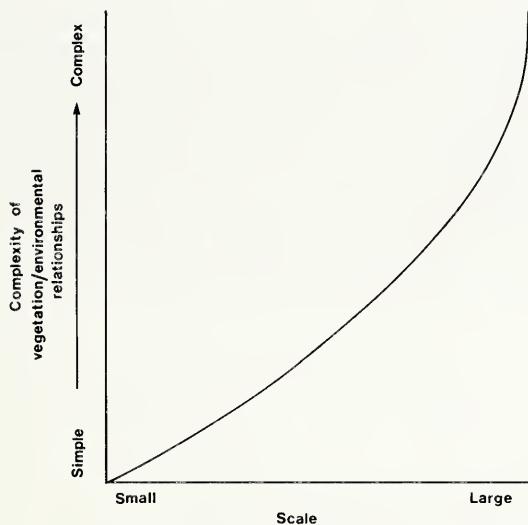


FIG. 23.—An idealized relationship between complexity of vegetation/environmental relationships and scale.

In southern Africa the possible attributes of floristic samples are the approximately 22 000 species and 2 000 infraspecific taxa found in the area, whereas the attributes of structural samples are currently in the order of a few to hundreds. It is, therefore, not surprising that floristic classifications do not generally correspond well with structural classifications.

The units used in floristic classifications that correspond approximately to the biome scale, are termed phytochoria (Werger 1978a). These phytochorial units would correspond better to biome units if the phytochoria were not subjectively derived but classified according to

rigorous phytosociological methodology with adequate sampling. In Fig. 24a the relation between mapping scale and number of structural forms and number of species is indicated for an idealized biome. The increase in species number with decreasing scale is considerably more gradual than that for the fewer number of available structural forms, before attaining the same relative asymptote. The degree of non-correspondence between floristic and structural units for the same range of scales is given in Fig. 24b. Correspondence decreases steadily with larger mapping scales until minimum correspondence is reached at a small floristic unit. With smaller units, correspondence increases rapidly until maximum correspondence is reached with individual plants. It is clear that, for all

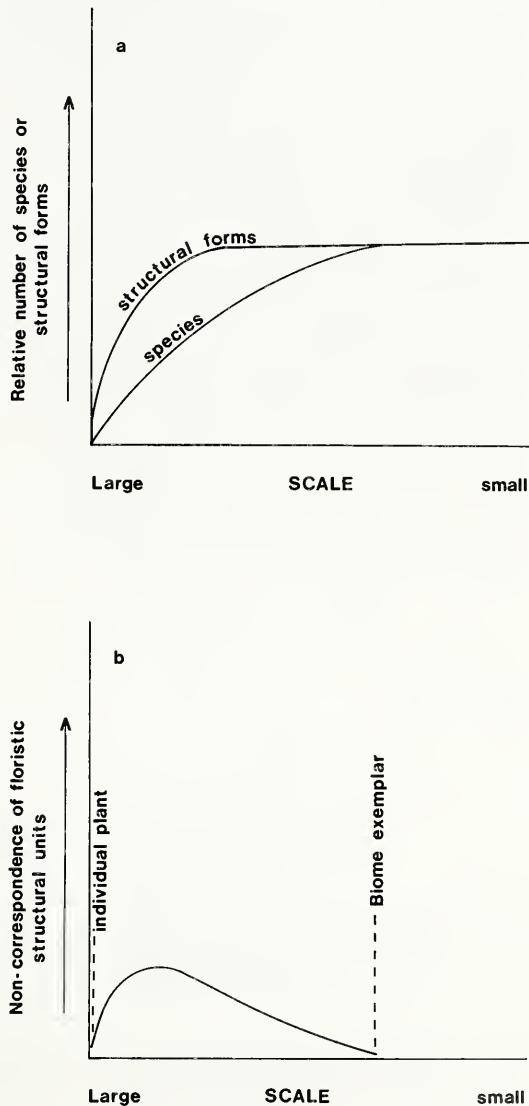


FIG. 24.—Generalized relationships between: a, relative number of species or structural forms and scale; b, non-correspondence of floristic structural units and scale. Correspondence between floristic and structural units is greatest at the individual plant and very small scale.

practical mapping scales, maximum correspondence between floristics and structure occurs at the biome scale within a subcontinent. From Fig. 24a it is also evident that sampling requirements for a biome are considerably less than for the corresponding phytocorion owing to the differences in the rates with which the asymptotes are reached. This explains how it has been possible to categorize biomes before the objective categorization of floristic units at this scale.

The curve in Fig. 24b represents an idealized relation. However, floristic spatial concentrations usually result in modification of the relation between scale and correspondence between floristic and structural units (Fig. 25). This modified curve results from species increases after the initial species saturation has been reached with increasing area within the biome. For biomes of small area, the curve segments (Fig. 25) usually do not correspond to phytocoria as defined by White (1983). However, for biomes of large area, the curve segments may correspond to such phytocoria and the biome concerned consequently contains several such phytocoria. This pattern in large biomes, for example, the Savanna Biome, may relate to the role of distance as an isolating factor for speciation in the biome with its relatively uniform environment. The problem of species vicariance in categorizing phytocoria may be partly explained by this factor. The problem may be ameliorated by selective recourse to taxa of higher rank. Where structural vegetative characters and combinations thereof for plants are skilfully selected to be species-diagnostic, the correspondence of floristics and these structural units is close (Werger & Sprangers 1982), as may be expected, and Figs 24a & 25 are irrelevant. Such choice of structural characters simply replaces the classification based largely on reproductive organs. Use of this type of structural character is practical at large scale but impracticable at

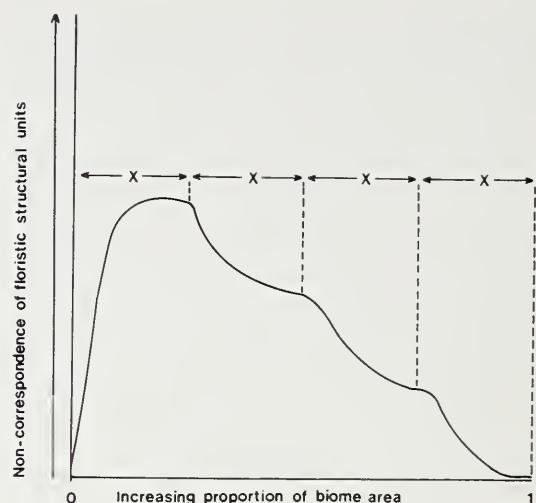


FIG. 25.— Generalized relationship between non-correspondence of floristic structural units and increasing proportion of biome area. X: segment representing area of change in floristic composition sometimes associated with a centre of endemism. For large mapping area X = possible area of endemism; for small mapping area X = change in floristic composition.

small scale mapping of large areas, for example, biomes. Species distributions of a selected growth form have been used to determine phytocoria. For southern Africa, Knight *et al.* (1983) have used species distributions of the tree form to delimit six major tree provinces using standard analytical methods. Any relation between these provinces and phytocoria are, however, subject to the distributional patterns of the remaining approximately 94% of vascular plants in southern Africa. More important is that the tree form is biased towards certain environmental zones and does not have an equitable chance of

TABLE 10.—Attributes used in the divisive classification of areas at different levels of detail or scale

Level of detail	Mapping concept	Attributes	
		Biotic	Abiotic
I	Biome	Dominant plant life forms  (Life form which is approximated by plant height and relative mean annual productivity of each life form which is often reflected by relative projected canopy cover)	Climate  (Rainfall seasonality, summer drought index, minimum temperature)
II	Major Biomic subdivision	Total mean annual primary productivity which is approximated by the total projected canopy cover of the life forms	Climate (mean annual rainfall)  Pedogenesis
III	Vegetation formation	Finer divisions of plant life forms, growth forms, height and cover	Local climate (includes topographic influence)  Pedogenesis

— Direct interdependence between main attributes

- - - - Indirect interdependence between main attributes

occurrence in all major regions of southern Africa. It is not unexpected that the use of tree forms (on a fairly coarse geographical grid) does not identify grassland units.

The division of biomes into smaller structural units (see Section 4) and correlation with abiotic attributes is illustrated in Table 10. Although it could be expected from Fig. 23 for the abiotic attributes of Level II to be applicable to Level I, the difference in complexity of these attributes is not great when compared with the possible complexity in Level III and levels of greater detail (Table 10). Furthermore, the simpler attributes of Level II are not used in the initial categorization because: 1, the acceptable biome definition is as in Level I; 2, use of the attributes of Level I results in a determinate number of possible biomes, whereas use of the attributes of Level II in the initial categorization would result in an indeterminate number of possible biomes and the biomes would depend

solely on arbitrary subdivisions of these attributes; and 3, the resulting biomes could include extremely high biotic structural diversity. Divisions of the biomes based on floristic criteria could be expected to have similar abiotic attributes to the structural divisions (Table 10) although the borders of the floristic divisions need not necessarily correspond with those of the structural divisions.

There may be many who are disappointed in this work because they feel either that 'their' geographical areas has been superficially treated or that the content does not meaningfully compare the ecosystem processes of biomes. To these we must reiterate that, despite shortcomings of the present work, they may have failed to grasp the fundamental hierarchical concept of scale or detail. In sciences with a large range of spatial sizes, scale is part of truth itself.



## 7 Conclusions

(1) The primary basis for distinguishing biomes is elegantly simple and permits equitable and valid categorization of major natural systems.

(2) In terms of hierarchical theory, consideration of the reduction of information at increasingly higher hierarchical levels is essential for assessing the correct status of biomes.

(3) Vegetation structure and floristic units are scale-dependent and the relationship between the two is therefore also scale-dependent.

(4) Irrespective of the selected parameters, all vegetation must be considered, to obtain the necessary holistic view for valid categorization of biomes.

(5) The existence of the narrow intermediate chamaephyte class, between ground level (with hemicryptophytes) and the wide and open-ended class of larger erect plants (phanerophytes), is climatically highly significant and is essential for distinguishing many highly distinct biomes.

(6) Diversity of morphological and functional adaptation of plants is negatively related to warm season precipitation. The variation within a plant life form increases in areas of greater environmental stress.

(7) The number of combinations of dominant life forms (biomes) is greatest at mid-latitude positions, owing to greatest climatic diversity between the tropical and polar air masses.

(8) Intercontinental biome comparisons can be made but correlations between dominant life forms and major climatic features are not necessarily iden-

tical globally owing to possible divergent evolution of taxa.

(9) The application of the refined concept of desert does not afford desert biome status to many areas previously described as 'deserts'.

(10) The bioclimatological index used in the present work serves as a model to effectively use very limited climatic data networks.

(11) All except one of the eight possible biomes defined in terms of important life forms occur in southern Africa south of 22°S. The 'missing' biome, where chamaephytes and phanerophytes are codominant, appears to be of very limited extent globally.

(12) The hitherto least recognized biome, namely Succulent Karoo, has had its biome status fully justified in the present study.

(13) The influential work of Acocks (1975) over-emphasizes the supposed prior condition of many veld types which he calls false. However, in the light of this study, few such claims are tenable in terms of biomes. The claims are supported by bioclimatological and other evidence only in the central and eastern parts of Veld Type 36 (False Upper Karoo).

(14) Before the zoological component can be adequately evaluated in biome context, greater attention must be given to environmental and trophic relations of all animals in given areas.

(15) For the subdivisions of biomes, there is a need for an unbiased, ecologically based soil classification that takes into account vegetation hierarchies.

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# Appendices

## APPENDIX 1 : COMPLETE LIST OF RAINFALL STATION NUMBERS (S.A. WEATHER BUREAU) AND STATION NAMES USED FOR BIOME CORRELATION IN FIG. 10

0001/517	Danger Point – VRT	0014/393	Harkerville – BOS
0001/605	Gansbaai	0014/633	Plettenbergbaai – POL
0002/069	Peters Gate	0016/484	Klipdrift
0002/256	Quoin Point – BOS	0017/452	Humansdorp – POL
0002/639	Voëlvlei	0017/486	Sanddrift
0002/885	Zoetendalsvallei	0020/689	Table Mountain – Woodhead Tunnel
0003/192	De Mond – BOS	0020/716	Cape Town – Tamboerskloof
0004/694	Silvermine	0020/719	Table Mountain – Disa Head
0004/702	Kogelfontein	0020/746	Table Mountain – Lower RSV
0004/721	Eagles Nest	0020/746A	Table Mountain – Molteno RSV
0004/723	Tokai – BOS	0020/747	Table Mountain – Platteklip
0004/762	Simonstown – MUN	0020/748	Table Mountain – Waaivlei
0004/826	Smitswinkelbaai	0020/778	Table Mountain – Maclears Beacon
0004/874	Rondevlei	0020/807	Table Mountain – Devils Peak
0005/034	Zeekoevlei	0021/055	Cape Town – Maitland – CEM
0005/611A	Steenbras No. I – RSV.	0021/130	Van Schoorsdrift
0005/612	Steenbras No. II – RSV	0021/204	Belville – SAR Kwekerye
0005/730	Steenbras No. IV – RSV	0021/205	Hardekraaltjie
0005/759	Steenbras No. V – RSV	0021/235	Belville – BOS
0005/771	Betty's Baai	0021/441*	Kraaifontein – BOS
0005/849	Steenbras No. VII – RSV	0021/809	Jonkershoek – 2D
0005/880	Morning Star	0021/838	Jonkershoek – 4M
0006/039	Grabouw – BOS	0022/099	Onverwacht
0006/051A	Kleinmond – POL	0022/104	Keerweder
0006/065	Nieuweberg – BOS	0022/113	La Motte – BOS
0006/167	Highlands – BOS	0022/116	Driefontein – BOS
0006/192	Lebanon – BOS	0022/204	Franschoek
0006/214	Rus-en-Vrede	0022/368	Swartvlei
0006/232	Middelvlei – BOS	0022/471	Stettynskloof
0006/415	Hermanus – MUN	0022/504	Welgegund
0006/612	Boontjieskraal	0022/539	Villiersdorp
0007/050	Dunghye Park	0022/759	Worcester – TNK
0007/106	Ysbrandskop	0022/792	Brandvleidam
0007/263	Boskloof	0022/803	Doornrivier
0007/311	Windheuwel	0023/100	Onderplas
0007/595	Mierkraal	0023/597	McGregor – POL
0007/718	Napier – POL	0023/706	Mont Blois
0007/828	Klipdale – SAR	0023/602	Soutrivièr
0008/136	Protem – SAR	0023/629	Rhebokskraal
0008/367	Kleinfontein	0024/101	Middelvoëtpad
0008/470	Plaatjeskraal	0025/162	Bellair dam
0008/751	Swilendam – BOS	0025/270	Zuurbraak
0009/365	Van Reenens Crest	0025/451	Anysberg
0009/430	Oudekraalskop	0025/484	Platdrift
0009/815	Heidelberg C/K – POL	0025/599	Strawberry Hill – BOS
0010/456	Riversdale	0026/215	Algernyskraal
0010/575	Fairview	0026/240	Correnerivier
0010/742	Stilbaai – BOS	0026/510	Garcia – BOS
0011/065	Diepkloof	0026/824	Vanwyksdorp – POL
0012/125	Geelbecksvlei	0027/876	Welbedag
0012/220	Mosselbaai – MAG	0028/083	Ruiterbos – BOS
0013/873	Belvedere	0028/130	Amoed – Noord
0014/063	Knysna – TNK	0028/207	Pine Grove – BOS

0028/407	Groot Doornrivier	0042/280	Remhoogte
0028/415	Jonkersberg – BOS	0042/292	Artois
0028/536	Kleinfontein	0042/325	Kluitjeskraal – BOS
0028/650	Wagenboomskraal	0042/355	Woiseley – POL
0028/771	Herold – POL	0042/357	La Plaisante
0028/775	Witfontein – BOS	0042/415	Waverley Mills
0028/842	Le Roux – SAR	0042/529	Vogelvlei
0029/058	Saasveld – BOS	0042/581	Bokveldskloof
0029/211	Aangenaam	0042/802	Agterfontein
0029/258	Schoonberg	0043/109	Klondyke
0029/291	Kleinplaat – BOS	0043/239	Orchard
0029/294	Bergplaats – BOS	0043/566	Matroosberg/Helpmekaar
0029/297	Woodville – BOS	0043/516	Spes Bona
0029/450	Swartvlei	0044/286	Jan-de-Boers
0029/534	Geelhoutboom – BOS	0044/765	Pieter Meintjies – SAR
0029/542	Rooirivier	0045/134	Matjiesfontein – SAR
0029/556	Molenrivier	0045/184	Dwars-in-die-Weg
0029/624	Karatara – BOS	0045/224	White Hill – SAR
0029/684	Farleigh – BOS	0045/611	Laingsburg – MUN
0029/692	Buffelsklip	0045/630	Prinsrivier
0029/805	Goudveld – BOS	0046/457	Koup – SAR
0029/821	Rooiplaas	0046/898	Opsoek – POS
0029/863	Millwood – BOS	0047/436	Weitevreden
0030/073	Wolwekraal	0047/567	Groenfontein
0030/088	Gouna – BOS	0048/043	Prince Albert – TNK
0030/090	Concordia – BOS	0048/275	Zachariasfontein
0030/212	Vetvlei	0048/449	Schoemanshoek
0030/219	Uniondale TNK	0049/050	Klaarstroom – POL
0030/265	Buffelsnek – BOS	0049/071	Zwartskraal
0030/283	Avontuur – SAR	0049/092	Zeekogat
0030/323	Rooimuur	0049/372	Rondawel
0030/390	Kafferskop – BOS	0049/562	Matjesvlei
0030/446	Kransbos – BOS	0049/834	Milnersdale
0030/493	De Hoop	0049/868	Rooikrans
0030/764	Ongelogen	0050/230	Tuintjieskraal
0030/775	Keurboomsrivier – BOS	0050/308	Slabbertspoort
0031/167	Kleinrivier	0050/527	Middelkraal
0031/237	Bloukrans – BOS	0050/785	Volstruisleegte
0031/438	Krakeelrivier	0050/887	Willomore – MUN
0031/507	Lottering – BOS	0051/285	Lomar
0031/619	Joubertina	0052/270	Koeifontein
0032/173	Hendrikskraal	0052/590	Steytlerville – MAG
0032/209	Witelsbos – BOS	0053/055	Schuinspad
0032/275	Zandvlakte	0053/274	Volstruiskop
0032/408	Nooitgedacht	0053/432	Eenstroon
0032/481	Rooikrans	0054/177	Morgenpracht
0032/503	Zuur Anys	0055/410	Zuurberg – BOS
0032/507	Kareedouw – POL	0056/139	Aicedale
0032/894	Dawkomskraal	0056/532	Carlsrust
0033/384	Langhoogte	0056/709	Fir Glen
0033/680	Hankey – POL	0056/737	Slaaikraal
0033/774	Buffelshoek – SKL	0057/048A	Grahamstown – TNK
0033/811	Sleutelpoortjie	0057/108	Sunnyside
0034/047	Otterford – BOS	0058/327	Lessendrum
0034/121	Adolphskraal	0058/334	Line Drift
0034/138	Loerie – BOS	0059/043	Released Areas – 33
0034/381	Van Staadens – RSV	0059/158	Richmond No. 69
0034/706	Uitenhage – TNK	0059/243	Silverdales
0035/060	Emerald Hill	0060/780	Saldanha – POL
0035/341	Tankatara	0063/718	Excelsior
0035/605	Arizona	0066/027	Oumure
0036/397	Hillcrest	0067/074	Anysrivier
0036/642	Alexandria – BOS	0067/279	Vanwyksplaas
0036/698	Welbedacht	0067/704	De List
0036/729	Alexandria – POL	0068/010	Merweville – POL
0037/039	Spadona	0068/061	Wilgeboschdrift
0037/282	Boesmansriviermond	0068/329	Prince Albert Road – SAR
0040/035	Langebaan – POL	0068/547	Zeekoevlei
0040/146	Dassen Island – VRT	0068/589	Wilgerfontein
0040/604	Hopefield – POL	0068/594	Zwartz – SAR
0040/875	Vlakvlei	0068/857	Leeu Gamka – SAR
0041/417	Malmesbury – TNK	0069/483	Letjiesbos – SAR
0041/684	Kloovenburg	0069/559	Lammerkraal
0041/836	Rondeheuwel	0069/674	Bakovenvontein
0041/871	Porterville – MUN	0069/856	Knapdraai
0041/885	La Bonne esperance	0070/033	Cypherfontein
0042/166	Mont Pellier	0070/093	Noblesfontein
0042/201	Waterfall – BOS	0070/735	Klipkrans
0042/227	Tulbagh – POL	0071/106	Middelkraal

0071/121	Verekul	0090/176	Grootfontein
0071/264	Rietbron – MUN	0090/196	Tafelberg
0071/337	Wiegaarspoort	0090/600	Bulwater
0071/626	Makouwkuil	0090/673	Rietvlei
0072/662	Skoongesig	0091/288	Grantham
0073/501	Oatlands	0091/516	Matjesfontein
0073/871	Kendrew estates	0091/763	Paardekraal
0074/256	Uitkomst	0091/782	Rosedene
0074/296	Jansenville	0091/835	Klipbanksfontein
0074/296A	Jansenville – POL	0091/896	Weltevrede
0074/363	Klipfontein	0092/180	Lombardskraal
0075/090	Biejesfontein	0092/369	De Hoop
0075/215	Pearston – POL	0092/386	Blouboskuil
0075/745	Die Hoogte	0093/005	Nelspoort
0076/215	Oukraal	0093/070	Nelspoort
0076/567	Middleton – SAR	0093/074	Kamferskraal
0076/884	Albertvale	0093/314	Bakensrug
0077/522	Adelaide – POL	0093/580	Poortjie-wes
0077/881	Fort Fordyce – BOS	0094/167	Sarelrivier
0078/153	Buxton – BOS	0095/006	Quaggasdrift
0078/214	Buxton	0095/119	Aberdeen – TNK
0078/226	Fort Beaufort – POW	0095/123	Doornbosch
0078/227	Fort Beaufort – TNK	0095/273	Zuurplaats
0078/271	Ubique	0095/395	Houd Constant
0078/296	Merino	0096/045B	Graaff Reinet – SAR
0078/755	Hogsback – BOS	0096/094	Groothoek
0078/859	Middeldrift	0096/272	Bloemhof
0078/860	Middeldrift – SAR	0096/366	Glen Harry
0078/879	Wolfridge – BOS	0096/551	Excelsior
0079/073	Lenye – BOS	0097/239	Walsingham 1
0079/200	Fort White	0097/252	Blinkberg
0079/215	Cata – BOS	0097/332	Kareefontein
0079/251	Keiskammahoek – POL	0097/750	Die Dorings
0079/396	Dontsa – BOS	0097/859	Honey Grove
0079/485	Kubusie – BOS	0098/184	De Doorns
0079/490	Isidenge – BOS	0098/412	Semaphore
0079/507	Orange Grove	0098/475	Cloverfields
0079/518	The Willows	0098/487	Plankfontein
0079/523	Evelyn Valley – BOS	0098/553	Lake Arthur dam
0079/524	Pirie – BOS	0098/638	Rietfontein
0079/524A	Maden dam	0098/793	Elandsdrift
0079/551	Cwencwe – BOS	0099/020	Leliekloof
0079/632	Kologha – BOS	0099/102	Hartbeesleegte
0079/683A	King Williamstown – TNK	0099/305	De Hoop
0079/721	Alta	0099/496	Spring Valley
0079/730	Izeleni – BOS	0099/622	Ventnor
0079/754	Stutterheim – TNK	0099/691	Drummond Park
0079/754A	Stutterheim – Wylde	0099/811	Rocklands
0079/782	Dohne – SAR	0100/025	Fountain Head
0079/815	Kubusie – SAR	0100/060	Millholme
0079/823	Frankfort – C/K	0100/176	Stonehouse
0080/052	Blaney	0100/293	Hex Plantation
0080/072	Kei Road – POL	0100/487	Brakkloof
0080/143	Berlin – SAR	0100/535	Otterburn
0081/013	Mooiplaas	0100/550	Whittlesea – POL
0081/255	Inyara – BOS	0100/617	Waterdown dam
0081/435	Haga – HAGA	0100/779	Rockford
0081/758	Qolora Mouth	0101/444	Crawley
0083/515	Lambertsbaai – POL	0101/641	Hotfire
0084/059	Redelinghuys – POL	0101/660	Hurst
0084/159	Graafwater	0101/688	Toise river
0084/558	Elandsfontein	0101/719	Fort Cunyngham – BOS
0084/701	Clanwilliam – POL	0101/804	Qacu – BOS
0085/112	Algeria – BOS	0102/762	Ngamakwe – TNK
0085/162	Heuningvlei – BOS	0102/840	Kei Bridge
0085/309	Mertenhof	0103/230	Butterworth – TNK
0086/007	Reenen	0103/516	Idutywa – TNK
0086/079	Elandsvlei	0104/206	Manubie – BOS
0087/164	Roodewerf	0106/408	Doringbaai
0087/186	Agterkop	0106/425	Ebenezer – COL
0087/519	Meintjiesplaas	0106/512	Koekenaap – IRR
0087/586	Voëlfontein	0106/603	Lutsville – POL
0087/635	Bet-El	0107/318	Puts
0088/293	Sutherland	0107/396	Van Rhynsdorp – TNK
0088/667	Prinshof	0107/510	Bulshoek – IRR
0089/038	Fonteinplaas	0107/761	Diepvlei
0089/385	Rhenostervlei	0107/867	Knolvlei
0089/693	Grootfontein	0108/311	Loekenburg
0089/894	Rondom	0108/418	Doornbosch

0109/122	Wilgenbosch	0123/512	Kalkoenkrans – POL
0109/215	Platberg	0123/654	Queenstown – TNK
0109/550	Kreitzberg	0124/402	Lady Frere – TNK
0109/588	Vondelingsfontein	0124/666	Eiffel
0109/835	Die Hoop	0125/150	Cofimvaba – TNK
0109/853	Rooiwal	0125/331	Cala – TNK
0110/512	Diepdrift	0127/298	Elliottdale – TNK
0110/649	Harderug	0128/040	Ngqeleni – TNK
0111/138	Bonekraal	0129/068	Port St Johns – POL
0111/373	Daniels Hope	0131/170	Swartbooisvlei
0111/789	De Puts	0131/437	Elandsfontein
0112/174	Sonop	0131/639	Nuwerus – POL
0112/346	Ploegfontein	0131/767	Grootgraafwater
0112/611	Hongerfontein	0133/050	Cloudskraal
0112/672	Rusoord	0133/344	Doornrivier
0113/043	Wamakersvlei	0134/378	Groot Toren
0113/321	Spitshoek	0134/478	Calvinia – TNK
0113/330	Ratelfontein	0134/854	Manelsfontein
0113/673	Saaifontein	0135/836	Oukoppieskraal
0113/711	Hereneging	0136/367	Bordeaux
0114/505	Driefontein	0136/741	Willeston – SAR
0114/597	The Rosary	0137/337	Grootfontein
0114/649	Snydersfontein	0137/614	Skuinhoopte
0114/700	Slangfontein	0138/030	Springfontein
0114/703	Rocklands	0138/041	Goraas
0114/747	Dunedin	0138/062	Scorpiendrift
0114/815	Lakenvlei	0138/204	Rheboksfontein
0115/324	Harmutspoort	0139/033	Celleryfontein
0115/528	Wagenaarskraal	0139/089	Visgat
0115/595	Gannakraal	0139/658	Loxton – POL
0116/029	Kromrivier	0139/850	Prinshof
0117/196	Allemansfontein	0140/003	Beyersfontein
0117/487	Elandspoort	0140/020	Rietfontein
0117/675	Klipplaat	0140/207	Boshoek
0118/370	Augustkraal	0140/582	Kweekwa
0118/395	Zoetvlei	0140/616	Sterling
0118/694	Dassiesfontein	0140/649	Eden
0118/782	Leopardsvlei	0141/066	Rheboksfontein
0119/082	Nieu-Bethesda – POL	0141/204	Victoria West – TNK
0119/097	Donkerhoek	0141/307	Kalkfontein
0119/130	Good Hope	0141/329	Biesjesfontein
0119/243	The Willows	0142/153	Lekkervlei
0119/315	Gordonville	0142/158	Beskuitkuil
0119/401	Coetzeesfontein	0142/210	Rondawel
0119/736	Rooihoopte – SAR	0142/248	Selbourne
0120/146	Kleinfontein	0142/262	Klipkraal
0120/243	Greyville	0142/379	Patrysfontein
0120/249	Stradbroke West	0142/497	Oufontein
0120/308	Stradbroke	0142/805	Richmond C/K – TNK
0120/338	Tafelberg Hall	0142/853	Die Aarplaas
0120/351	Doringkuil	0143/218	Wortelfontein
0120/721	Culmstock	0143/258	Scheurfontein
0120/745	Fish River	0143/294	Nooitverwacht
0120/838	Fortuinplaas	0143/345	Grootfontein
0120/876	De Keur	0143/579	The Mills
0121/191	Teviot	0143/598	Middlemount
0121/275	Kareefontein	0143/784	Hanover – POL
0121/370	Varsvlei	0143/853	Hoogmoedsfontein
0121/421	Tafelkop	0144/085	Bokfontein
0121/518	Hofmeyer – MUN	0144/182	Droogefontein
0121/547	Montana	0144/250	Vrede
0121/565	Newlands	0144/253	Gordonsfontein
0121/574	Bloemhof	0144/266	Paardevlei
0121/598	Grootdam	0144/534	Uitzicht
0121/745	Kenilworth	0144/580	Damfontein
0121/769	Leeuwkuil	0144/602	Moria
0121/787	Besterstad	0144/795	Carlton – SAR
0121/827	Grootvlei	0144/900	Middelburg C/K – TNK
0121/862	Erfdeel	0144/900A	Middelburg C/K – Stahl
0122/071	Smoordrif	0144/900B	Middelburg C/K – SAR
0122/351	De Hoek	0145/261	Telpoort
0122/428	Roetschoek	0145/399	Grapevale
0122/469	Elandsfontein	0145/810	Manor Holme
0122/514	Wildeperdehoek	0146/052	Hillston
0122/603	Burnley	0146/071	Pylfontein
0122/662	Kings Glen	0146/129	Springfield
0122/806	Waverley	0146/274	Verstersfontein
0123/063	Sterkstroom – POL	0146/382	Thebus waters
0123/111	Alphen	0146/765	Rietbron

0146/796	De Dam	0172/589	Brandwag
0147/135	Kalkoenkrans	0172/724	Tweefontein
0147/170	Zuurfontein	0172/814	Summerhill
0147/338	Erinmore	0172/818	Norvalspont – POL
0147/398	Mooivlei	0173/134	Montagu
0147/416	De Rust	0173/266	Doornkloof
0147/458	Mooifontein	0173/274	Gruisfontein
0147/599	Dalkeith	0173/430	Klipfontein
0147/631	De Villiers	0173/475	Elandsfontein
0147/654	Molteno – MUN	0173/497	Venterstad – MAG
0147/777	Syfergat – SAR	0173/553	Zeekoeagatboven
0148/083	Marshmoor	0173/652	Voëlfontein
0148/352	Buffelsfontein	0173/722	Lucknow
0148/401	Spitskop	0173/760	Vaalbank
0148/480	Halseton – SAR	0173/899	Skilderkrans
0148/517	Jamestown – POL	0174/017	Cheviotdale
0148/525	Den Haag	0174/032	Eerstestap
0148/530	Horatio	0174/056	Pleisterkraal
0148/532	Snymanskraal	0174/070	Stille Woning
0148/789	Swakfontein	0174/076	Damplaas
0149/025	Klein-Naauwpoort	0174/093	Clifton Vale
0149/052	Dordrecht – SAR	0174/205	Winnabaansbaken
0149/082	Dordrecht – TNK	0174/281	Deelsvlei
0149/165	Kransfontein	0174/312	Hughenden
0149/547	Siberia	0174/387	Die Tuine
0149/598	Indwe – MUN	0174/463	Hoogstede
0150/581	Barkly Pass – POL	0174/550	Ellesmere
0150/620	Elliot – SAR	0174/590	Stoneycroft
0151/604	Maclear – MAG	0174/753	Goedemoed – POL
0151/604B	Maclear – MUN	0174/877	Sanddrift
0153/875	Flagstaff – TNK	0175/022	Welgedacht
0154/142	Lusikisiki – TNK	0175/056	Vetkraal
0154/279	Holy Cross Mission	0175/311	Aliwal North – SAR
0157/035	Sariesaam	0175/371	Aliwal North – TNK
0157/647	Twee Rivier	0175/585	Houtkraal
0157/753	Schuinskraal	0175/801	Waterval
0157/874	Garies – POL	0176/002	Broederstroom
0157/874A	Garies – POS	0176/052	Majuba
0158/087	Rietpoort	0176/532	Motkop
0159/104	Kamaboes	0176/735	Ossa
0160/807	Loeriesfontein – POL	0177/178	Barkley East – TNK
0162/784	Nelskop	0177/184	Blikana
0163/141	Grootvolstruisfontein	0179/864	Mount Frere – TNK
0163/882	Brulpaddaleegte	0181/604	Glenora
0164/141	Witkalk	0182/710	Uvongo – MUN
0164/629	Klipkloof	0182/794	Port Shepstone – TNK
0165/003	Kleindubbelsvlei	0184/499	Hondeklipbaai – POL
0165/580	Jagersberg	0185/023	Wallekraal – SKL
0165/898	Carnarvon – AGR	0185/492	Grootvlei
0166/041	Garstkolk	0185/646	Kameelboom
0166/238	Carnarvon – SKL	0185/712	Kharkhams
0166/755	Oorlogshoek	0186/139	Kamiesberg
0167/264	Swaelfontein	0190/868	Brandvlei – POL
0167/665	Vosburg	0191/252	Onderstedoorns
0168/066	Sandpan	0191/526	Kraandraai
0168/250	Soutwater	0192/319	Blinkklip
0168/800	Nieuwejaarsfontein	0193/339	De Naauwte
0169/005	Britstown – POL	0193/347	Kalabasput
0169/090	Thomagat	0193/355	Gansvlei
0169/174	West Front	0193/561	Van Wyksvlei
0169/509	Deelfontein	0194/323	Gannapan
0170/085	Ezelsfontein	0194/454	Irene
0170/137	Hartebeesthoek	0195/730	Nooitgedag
0170/269	Rasfontein	0196/157	Omdraaisvlei
0170/315	Rietfontein	0196/251	Sodium
0170/584	Burgerville	0196/375	Rooipoort
0170/639	Rooiwal	0197/238	Doornkuil
0170/885	Sterkfontein	0197/342	Wildebeeskooi
0170/889	Theefontein	0197/713	Kocksbeen
0171/117	Wolmada	0198/292	Strydam
0171/508	Schuilhoek	0198/430	Vredehof
0171/546	Bell Rock	0198/435	Donkerhoek
0171/652	Mooifontein	0198/524	Basberg
0171/756	Esperanza	0198/836	Philipstown – TNK
0171/766	Middelwater	0199/107	Groot-Arendskraal
0172/027	Arundel	0199/222	Macasserpontein
0172/163	Colesberg – TNK	0199/275	Petrusville – POL
0172/324	Poplar grove	0199/293	Garsfontein
0172/580	Agtertang	0199/894	Olivewood

0200/058	Fonteintjie	0224/163	Môrewag
0200/166	Kareepoort	0224/389	Grootmodderfontein
0200/180	Diyatalawa	0224/430	Prieska
0200/255	Hartmanshoop	0224/430A	Prieska – MUN
0200/361	Philadelphia	0224/734	Uniteit
0200/465	Rowlesfontein	0225/065	Rooisloot
0200/488	Avondzon	0225/118	Kleindoornberg
0200/516	Bloemhof	0225/311	Graspan
0200/579	Alwynskop	0225/413	Lammertjiespan
0200/728	Mauritzkop	0225/679	Kareekloof
0200/743	Pienaarfontein	0225/792	Spioenpan
0200/746	Vlakfontein	0226/327	Strydenburg – POL
0200/764	Krielsfontein	0226/572	Van Tonderskrans
0200/791	Phillipolis road	0226/622	Elandsberg
0201/020	Oranje	0226/771	Goedehoop
0201/130	Baghdad	0227/054	Perdeput
0201/175	Priors – SKL	0227/127	Hopetown – TNK
0201/217	Blaauwheuwel	0227/558	Bakovenspan
0201/323	Excelsior	0227/643	Zoutpansdrift
0201/361	Hamelfontein	0228/187	Legpan
0201/370	Highbury	0228/327	Vissersdrift
0201/373	Hamilton Manor	0228/339	De Kroon
0201/376	Springfontein – MUN	0228/567	Tevredenheid
0201/464	Oaklands	0228/571	Adamshoop
0201/482	Trompsburg – POL	0228/657	Boshoffsdam
0201/492	Normandale	0228/710	Spitzkop
0201/637	Westward Ho	0228/725	Uitkyk
0201/701	Middelfontein	0228/783	Rietput
0201/762	Abercairn	0229/086	Kafferfontein
0201/775	Driefontein	0229/089	Mimosa
0201/840	Bethulie – MUN	0229/124	Taaiboslaagte
0201/843	Waterval	0229/170	Wheeldon
0202/261	Goedehoop	0229/215	Constantia
0202/359	Winterhoek	0229/265	Parys
0202/377	Haasfontein	0229/344	Sandymount Park
0202/505	Ebenhaezer	0229/475	Bokpos
0202/680	Lourensa	0229/555	Fauresmith – SKL
0202/687	Kareekloof	0229/571	Ventersvlei
0203/043	Smithfield – MUN	0229/579	Steenbokvlakte
0203/170	Bosrand	0229/629	Spitskop
0203/401	Excelsior	0229/654	Dwarsvlei
0203/483	Sonneblom	0229/723	Dassiepoort
0203/657	Middelpaats	0229/737	Jagersfontein – POL
0203/737	Riethoek	0229/862	Sluelpoort
0204/050	Leeuwfontein	0230/011	Gleniffer
0204/058	Compton	0230/027	Swartkoppies
0204/138	Zastron – TNK	0230/048	Middelfontein
0204/182	Boesmanskop	0230/073	Slangfontein
0204/265	Zondagsfontein	0230/074	Grasvlei
0204/350	Geluksvlei	0230/129	Lokshoek
0204/418	Quaggafontein	0230/210	Skema
0204/444	Welgemoed	0230/254	Vendutiekop
0204/486	Waratah	0230/349	Fairview
0204/515	Clearwater	0230/363	Blesbokfontein
0204/518	Spring Valley	0230/466	De Put
0204/616	Kornetspruit	0230/542	Vaalbank
0204/819	Mohaleshoek	0230/566	Krugers
0205/085	Telleburg – POL	0230/598	Bloemhof
0207/560	Matatiele – TNK	0230/764	Edenburg – POL
0210/099	Ixopo – POL	0230/774	Uitkyk
0211/437	Scottburgh – MUN	0230/810	Lillydale
0211/663	Amanzimtoti – MUN	0230/816	Bethany
0213/129	Grootmis – SKL	0231/076	Toelooop
0213/888	Komaggas	0231/114	Knelpoort
0214/670	Springbok – TNK	0231/161	Puntjiesfontein
0214/752	Concordia – COL	0231/279	Reddersburg – POL
0220/195	Steynsvlei	0231/289	Kruidfontein
0220/360	Lemoenkop	0231/361	Hebron
0220/820	Knapzak	0231/395	Bulsfontein
0220/827	Kampe	0231/454	Ellerslie North
0222/187	Basterpan	0231/754	Blouboskop
0222/324	Sondagspan	0232/011	Bulsberg
0222/648	Stompoor	0232/018	Cyferfontein
0223/058	Juriesleegte	0232/083	Helvetia – POL
0223/287	Hedley Plains	0232/123	Roodepoort
0223/356	Grassmoor	0232/275	Dewetsdorp – POL
0223/588	Sunnyside	0232/895	Sweetwater
0223/707	Louretha	0232/898	Quilimane
0223/834	Boesmansberg	0233/211	Hobhouse – POL

0233/439	Mafeteng	0260/083	Small Heath
0233/747	Thabana Morena	0260/126	Belgrave
0234/150	Mpharane	0260/163	Koppiesdam
0238/045	Himeville – MAG	0260/208	Berlin
0239/421	Merrivale	0260/314	Lyons Rose
0239/518	Edendale	0260/424	Vaalbank
0239/574	Pietermaritzburg – Country Club	0260/445	Klippan
0240/649	Pinetown – MAG	0260/519	De Brug – POL
0240/891	Durban – Botanical Gardens	0260/555	Northfield
0241/068	Verulam – TNK	0260/660	Pakpoort
0241/082C	Durban Point Road – 5	0260/678	Kuilput
0241/302	Frasers	0260/715	Rustfontein
0242/644	Port Nolloth – VRT	0261/105	The Willows
0244/134	Anenous	0261/146 A	Kafferrivier
0244/283	Klipfontein	0261/175	Wonderklip
0245/808	Soutvlei	0261/183	Bainsvlei
0247/242	Pella	0261/203	Riversford
0249/367	Droëgrond	0261/266 A	Tygerpoortdam
0249/594	Sandkolk	0261/275	Vredenhof
0250/418	Kleinswartbas	0261/365	Bloemfontein – Bayswater
0251/261	Kenhardt – POL	0261/368	Bloemfontein – Kings Park
0251/430	Nougas Suid	0261/517	Bloemspruit
0251/476	Kromput	0261/518	Shannon
0251/674	Middelpos	0261/722	Mazelspoort Dam
0252/848	Kareelaagte No. 2	0261/890	Middelpoort
0252/894	Brakboschpoort	0262/069	Sannaspos
0253/174	Marydale – POL	0262/613	Thaba Nchu – MUN
0253/285	Vaalbuilt	0263/034	Lokoalo
0253/648	Koegasburg	0263/041	Tweespruit
0254/572	Goup	0263/280	Westminster Estate
0254/761	Rietkuil	0263/499	Kommissiepoort
0255/202	Nuwejaarskraal	0263/760	Ladybrand – BOS
0255/471	Saxendrift	0263/786	Modderpoort-Priory
0255/552	Oranjeoord	0263/792	Ladybrand – SKL
0255/882	Vaalkrans	0264/022	Botsabelo
0256/274	Buckland	0264/399	Teyateyaneng
0256/381	Gertspan	0266/296	Makhuleng
0256/453	Douglas – POL	0266/370	Meno
0256/483	Douglas – Die Erven	0266/646	Lelingoanas
0257/391	Plooysburg	0267/126	Mothebesoane
0258/079	Spreewfontein	0268/199	Highmoor – BOS
0258/164	Michville	0268/352	Kamberg – Nature Reserve
0258/182	Modderrivier – POL	0269/176	Lidgetton
0258/218	Klokfontein – IRR	0269/559	Karkloof
0258/272	Kalkdrift	0270/021	New Hanover
0258/306	Gannahoek	0271/099	Mapumulo – TNK
0258/335	Rietrivier – IRR	0271/500	Stanger
0258/339	Holpan – IRR	0272/121	Gingindhlouvu
0258/380	Waterval – Wes	0272/127	Amatikulu
0258/399	Klipfontein – IRR	0273/754	Oranjemund
0258/434	Pramberg	0275/179	Lekkersing
0258/434A	Pramberg – IRR	0276/072	Vioolsdrift
0258/458	Jacobsdal – POL	0279/497	Onseepkans – POL
0258/467	Gannahoek – IRR	0280/351	Skuitklip
0258/581	Wegdraai	0280/772	Bladgrond
0258/624	Boshoffshoop	0281/760	Aughrabies
0258/740	Nooitgedacht – IRR	0282/166	Kakamas – SKL
0258/812	De Kalk	0282/464	Vaalhoek
0258/827	Koppieskraal	0282/823	Keimoes – POL
0258/841	Alexandria	0283/098	Geelkop
0258/894	Koffiefontein – POL	0283/334	Louisvale
0259/002	Mount Duncan	0283/466	Rietfontein
0259/086	Uitdraai – IRR	0284/008	Thornlea
0259/102	Weltevrede	0284/361	Wilgenhoutsdrift – SKL
0259/278	Kroonplaas	0284/832	Groblershoop – POL
0259/323	Tafelkop	0286/170	Breckenridge
0259/348	Leyden	0286/300	Westfield
0259/480	Tembani	0286/497	Range
0259/578	Inhoek	0287/041	Onder – Ongeluk
0259/609	Langefontein	0287/138	Nietena
0259/727	Petrusburg – POL	0287/314	Reliance
0259/743	Kranshoek	0287/441	Griquatown – TNK
0259/752	Westhoek	0287/574	Leeuvlei
0259/855	Dankbaar	0287/885	Poplars
0259/881	Bestersput – AGR	0288/416	Kalkdam
0259/887	Shottermill	0288/528	Tweefontein
0260/004	Doornplaat	0288/788	Orange Gove
0260/030	Steunmekaar – POL	0289/102	Schmidtsdrif
0260/082	Evesbatch	0289/243	Muirton

0289/302	Caerwinning	0323/271	Tevredenheid
0289/403	Grootdam	0323/649	Newlands
0290/191	Platfontein	0323/698	Bellsbank
0290/444	Mauritzfontein	0323/820	Spitskop
0290/464A	Kimberley – POL	0324/135	Vaalboshoek
0290/560	Benfontein	0324/202	Rocklands
0290/810	Drieputts	0324/290	Barton
0291/032	Sterkstroom	0324/379	Windsorton – POL
0291/159	Kromrand	0324/449	Smithsdale
0291/245	Leeufontein	0324/561	Windsorton Road – SAR
0291/360	Groepunt	0324/607	Warrenton – MUN
0291/392	Boshof – TNK	0324/613	Content – SAR
0291/863	Halfweg	0324/725	Nazareth House Farm
0291/899	Katdoornput	0324/873	Just-my-luck
0292/089	Kelvedon	0324/888	Knapdaar
0292/446	Paardekraal	0324/889	Lusthof
0293/007	Middelkop	0325/317	Amandelboom
0293/106	Florisbad	0325/471	Bordeaux
0293/204	Donkerhoek	0325/811	Morsaf
0293/339	Salzmannspan	0325/816	Houmoed
0293/403	Vooruitsig	0326/668	Geluk
0293/514	Stille Woning	0326/855	Oranje
0293/568	Glen-College	0327/257	Bultfontein – SKL
0293/622	Karee	0327/784	Nelsdrift
0293/700	Aardoorns	0328/294	Abrahamshof
0293/792	Brandfort – MAG	0328/384	Theunissen – MUN
0293/868	Mooihoeck	0328/576	Virginia – PUR
0294/417	Francina	0328/726	Olivine
0294/500	Verkeerdevlei – POL	0329/146	Beddington
0295/001	Winburg – POL	0329/215	Ventersburg – MAG
0295/116	Excelsior – MUN	0329/271	Weltevreden
0295/760	Marquard – POL	0329/470	Bakenvlakte
0296/115	Clocolan – POL	0329/700	Skaapplaas
0296/682	Ficksburg – TNK	0330/199	Senekal – AGR
0296/767	Dwarskloof	0330/421	Roodepoort
0297/337	Fouriesburg – MAG	0330/699	Leuctra
0298/512	Witsieshoek	0330/797	Paul Roux – MUN
0298/545	Elizabeth Ross – HOSP	0331/068	Kaallaagte
0299/357	Cathedral Peak – Hotel	0331/554	Bethlehem – TNK
0299/614	Bergville – MAG	0331/828	Nil Desperandum
0300/358	Draycott	0332/103	Skalkie
0300/690	Estcourt – TNK	0332/349	Kestell – POL
0301/094	Fitty Park	0333/051	Rosedale
0301/795	Tugela Ferry – MAG	0333/196	Harrismith – MUN
0302/628	Kranskop – TNK	0333/682	Van Reenen – POL
0303/127	Nkandla	0333/803	Grosvenor Downs
0303/633	Springvale	0335/169	Wasbank
0304/446	Mtunzini – MAG	0335/250	Glencoe – MUN
0304/487	Lavoni	0335/746	Helpmekaar – POL
0304/593	Port Durnford – D – BOS	0336/863	Babanango
0305/167	Richards Bay – MUN	0337/022	Babanango
0305/193	Msingazi	0337/143	Babanango – POL
0312/397	Naruchas	0337/795	Mahlabatini – MAG
0312/422	Karasburg	0339/065	Hluhluwe – Game Reserve
0312/779	Khais Suid	0339/282	Lansdowne
0314/032	Heirachabis	0339/441	Dukuduku – BOS
0314/482	Ukamas	0339/538	Uloa
0314/577	Ariamsvlei	0339/681	St. Lucia Estuary – BOS
0316/061	Swartmodder	0339/734	Makakatana
0316/294	Lutzputs	0339/756	Fanieseiland
0317/447	Upington – TNK	0347/527	Blanksdam
0319/582	Grootkuip	0348/819	Duurdrift Noord
0319/882	Nokanna	0349/082	Noibis
0320/348	Dunmurray	0349/158	Blinkoog
0320/359	La Dauphine	0349/238	Kububost
0320/696	Compass	0350/113	Nabas
0320/828	Aucampsrus	0350/151	Nimmerrust
0321/032	Lohathla	0350/542	Dawignab Suid
0321/110	Postmasburg – POL	0351/708	Vrouenspan
0321/159	Manganore	0355/585	Pilanyan
0321/441	Tierkop	0355/655	Jones
0321/719	Rocky Flats	0355/808	Hartebeeshoek
0322/071	Daniëlskuil – POL	0356/080	Moeswal
0322/329	Papkuil	0356/261	Inglesby
0322/519	Surprise	0356/272	Mitcham
0322/648	Vaalpan	0356/285	Hopkins
0323/075	Koopmansfontein – POL	0356/348	Puduhusche
0323/144	Potfontein	0356/417	Olifantshoek – POL
0323/160	Koopmansfontein 1 – AGR	0356/636	Deben - POL

0356/712	Smythe	0402/164	Kopjesdam
0357/413	Khosis	0402/718	Vegkop
0357/592	Branksea	0402/827	Heilbron – TNK
0357/774	Greyling	0403/054	Schoongezicht
0358/263	Nelsonsfontein	0403/646	Turffontein
0358/349	Gezina	0403/886	Frankfort
0359/304	Reivilo	0404/145	Bieskop
0359/458	Olyfenfontein	0404/152	Villiers – POL
0359/808	Boetsap – POL	0404/614	Cornelia – POL
0360/512	Taung – POL	0405/295	Vrede – TNK
0361/061	Sweetwilliam	0405/632	Kromdraai – SAR
0362/002	Bosmansfontein	0406/138	Streepfontein
0362/466	Beeskraal	0406/190	Paardekop – SAR
0362/710A	Hoopstad – SKL	0406/312	Palmford
0362/884	Ellasrus	0406/607	Rietpoort
0363/398	Mooiveld	0408/798	Zaaiplaats
0363/651	Wesselsbron – MUN	0409/130	Sulphur Springs – POL
0364/322	Odendaalsrus	0409/460	Dwaleni
0364/728	Togekry	0410/132	Hluti
0365/031	Enkeldoorn	0410/515	Mkiwane
0365/538	Kleininbreek	0410/878	Ingwavuma – TNK
0366/117	Steynsrus – MUN	0411/175	Otobotini
0366/390	Komspuit	0412/052	Mseleni
0366/743	Lindley – MUN	0413/158	Diaz Point – VRT
0367/066	Lanquedoc	0415/045	Tsirub
0367/219	Petrus Steyn – MUN	0416/228	Tschanabis
0367/330	Deelpan	0416/368	Doorns
0367/602	Hooggelegen	0417/405	Konkiep
0367/768	Reitz	0419/182	Keetmanshoop – WK
0368/003	Tweeling – POL	0419/215	Keetmanshoop (Town)
0368/601	Roadside	0419/665	Eisenstein
0368/831	Warden – MAG	0420/214	Stampriet
0369/505	Verkykerskop – POL	0421/696	Salztal
0370/116	Brakkrans	0422/257	Aroab
0370/765	Newcastle – TNK	0422/538	Louwsvley
0371/579	Utrecht – TNK	0422/823	Erfdeel
0372/496	Vryheid – TNK	0423/044	Rietfontein – POL
0373/058	Gluckstadt – POL	0423/618	Kleinmier
0373/485	Louwsburg – MAG	0424/357	Witdraai – POL
0374/264	Nongoma	0424/509	Askham
0375/124	Ubombo – MAG	0427/083	Vanzilsrus – POL
0375/688	False Bay Camp	0428/838	Karlsruhe
0380/519	Rooiberg	0430/111	Longhurst
0382/612	Oase	0430/354	Masilubitsani
0384/023	Noachabeb	0430/888	Southey
0384/408	Rishow	0431/465	Mistake
0384/804	Nukois	0431/690	Vogelpan
0384/852	Naos	0431/820	Lourensgeluk
0385/233	Hangas	0432/136	Welgeleven
0387/240	Noenieput – POL	0432/196	Progress
0390/155	Totsplaas	0432/387	Vryburg – POL
0390/514	Matlapanen	0432/633	Stella – POL
0391/834	Whyenbah	0433/043	Schuinshoogte
0391/857	Dedebe – POL	0433/791	Delareyville – MUN
0392/148	Winton	0434/599	Vogelstruiskuil
0392/473	Diepwater	0436/297	Vaal Reefs West
0392/592	Smuts	0436/827	Machavie
0392/680	Heuningdraai	0437/105	Mooibank
0393/083	Milner	0437/163	Potchefstroom
0393/225	Kareepan	0437/214	Boskop
0393/382	Mount Roper	0437/660	Vrededorp – SKL
0393/476	Whitebank – Mine	0438/315	Barrage – RWB
0393/566	Whitebank – Mill	0438/553	Vanderbylpark – PUR
0393/662	Colville	0438/729	Vereeniging – POW
0394/574	Bothitho – POL	0438/734	Viljoensdrift – POL
0394/878	Boscobel	0439/755	Kraal – SAR
0395/483	Geluk	0439/769	Beerlaagte
0395/855	Scholtzfontein	0440/157	Rietbuilt
0396/271	Retreat	0440/621	Grootspruit
0396/284	Madrid	0440/767	Val – SAR
0396/454	Tierkloof – SKL	0441/309	Charl Celliers
0396/853	Spreeuwfontein	0441/523	New Denmark
0397/581	Schweizer Reneke – POL	0441/860	Rietvlei – SKL
0398/254	Hessie	0442/194	Morgenzon – MAG
0398/851	Wolmaransstad cupids valley	0442/660	Amersfoort – POL
0398/889	Makwassie	0442/898	Maquabie
0399/404	Leeudoringstad – SKL	0443/196	De Emigratie
0399/419	Commandodrift	0443/451	Blaakkop
0402/104	Koppies – IRR	0443/807	Brereton Park

0444/203	Idalia	0509/123	Zeerust – TNK
0444/277	Amsterdam – POL	0509/394	Vaalkop
0444/746	Blesbokspruit	0509/726	Groot Marico
0445/100	Mankayane	0510/308	Swartruggens – POL
0446/355	Poponyane	0510/410	Doornpoort
0446/773	Wisselrode	0510/712	Koster – POL
0447/446	Ndumu	0511/400	Rustenburg – POL
0448/450	Maputa	0511/418	Boons – POL
0448/597	Kosibaa	0512/344	Wolhuterskop
0454/270	Bethanien	0512/451	Rashoop – IRR
0456/027	Gellap – OST	0512/467	Scheerpoort
0458/639	Morgenson Suid	0512/481	Mamogaleskraai – IRR
0464/783	Tsabong	0512/488	Brits
0467/487	Morokweng – POL	0513/003	Hebron
0467/818	Donegal	0513/309	Onderste poort – VET
0468/210	Fielden	0513/350	Verwoerdburg – MUN
0468/500	Haarlem	0513/382	Irene
0469/359	Peachdale	0513/417	Olifantsfontein
0469/795	Zwartlaagte	0513/743	Tygerpoort
0471/618	Mimosa	0513/836	Welbekend – POL
0471/624	Doorndraad	0514/329	Waaikraal
0471/713	Biesievlei – POL	0514/408	Bronkhortspruit – MUN
0472/175	Rooijantjesfontein	0515/234	Clewer
0473/416	Klipplaatdrift – SKL	0515/382	Witbank – MAG
0474/020	Buckingham	0515/528	Olifantsrivier – SAR
0474/255	Klerkskraal – POL	0515/826	Middelburg – TNK
0474/270	Frederikstad – SAR	0516/708	Wonderfontein – SKL
0474/502	Welverdiend – POL	0517/072	Belfast – POL
0474/684	Blyvooruitsig – GM	0517/285	Dalmanutha
0474/899	Fochville – POL	0517/430	Machadodorp
0475/019	Bank – SAR	0517/669	Waterval Onder
0475/227	Venterspos – Old Homestead	0517/816	Elandshoek
0475/244	Tarlon	0517/877	Airlie – SAR
0475/370	Randfontein – GM	0518/072	Slaaihoek
0475/455A	Krugersdorp – POL	0518/088	Badplaas – POL
0475/669	Roodepoort – MUN	0518/455	Kaapsehoop
0475/710	Van Wyksrus	0519/572	Kaapmuiden
0475/761	Maraisburg – GM	0520/476	Border Gate
0475/881	Johburg – Braamfontein – CEM	0520/589	Fig Tree
0476/040	Johannesburg – Zoological Gar	0520/636	Squamans
0476/072	Johannesburg – Joubert Park	0526/679	Betta
0476/093	Sandton – POL	0527/430	Klein Fontein Noord
0476/317	Roodekop	0527/539	Osis
0476/396	Kemptonpark – SAR	0529/428	Gibeon
0476/644	Brakpan – MUN	0529/452	Gideon Reservaat
0476/736	Springs – RWB	0530/700	Welverdiend
0476/835	Nigel – 1	0531/037	Langerveld
0477/309	Delmas – POL	0540/620	Rusthof
0477/501	Devon – POL	0541/297	Bray – POL
0477/772	Leslie – MUN	0545/499	Gopane
0478/093	Ogies – POL	0545/626	Dinokona
0478/419	Trichardt	0545/663	Kalkpan
0479/297	Davel	0546/007	Swartfontein
0479/369	Hendrina – MUN	0546/272	Nietverdiend – POL
0479/858	Breyten – MUN	0546/525	Olifantsvlei
0480/184	Carolina – MUN	0546/687	Riekersdam
0480/377	Chrissiesmeer – POL	0546/712	Skuinsdrif – IRR
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0481/310	The Brook	0550/522	Pienaarsrivier
0482/690	Transvalia	0550/612	Kalkheuwel
0483/260	Panata	0550/666	Palmietgat
0483/426	Swaziland Ranch – Homestead	0551/013	Rust der Winter
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0506/386	Logaging	0554/682	Badfontein – POL
0507/716	Shopsite	0554/786	Lydenburg – POL
0508/261	Mafeking – TNK	0555/573	Klipkraal
0508/649	Slurry	0555/588	Rosehaugh – BOS
0508/825	Ottoshoop – POL	0555/608	Malieveldvallei – BOS

0555/837	Nelspruit – AGR	0654/646	Mbela
0555/878	Witwater – BOS	0654/802	Bitterwasser
0556/460	Pretoriuskop	0654/842	Rheinpfalz
0556/898	Malelane	0655/255	Ja Dennoch
0557/326A	Hectorspruit	0655/397	Derm
0557/712	Krokodilbrug	0655/503	Gomchanas Ost
0566/007	Kamkas	0656/028	Strate
0566/309	Karab	0656/541	Leonardville
0566/860	Maltahöhe	0656/582	Perdepan
0567/035	Sandhof	0656/771	Manie
0568/095	Haribes	0657/036	Uitkoms
0568/307	Dassiesfontein	0672/748	Cumberland – POL
0568/817	Mariental	0673/015	Wilton Valley
0569/271	Kouwater	0673/081	Ireland
0570/186	Kleinhutte	0673/128	Kruispad
0570/531	Gochas	0673/645	Zyferbult
0570/637	Duineveld	0674/207	Sterkfontein
0588/385	Leeupoort	0674/429	Grootfontein
0588/406	Rooiberg	0675/117	Derdekraal
0588/721	Rankinspass	0675/125	Autoriteit
0588/732	Kareefontein	0675/182	Villa Nora – POL
0589/298	Eeng gevonden	0676/523	Vaalpenskraal
0589/460	Vaalkop	0676/705	Swerwerskraal
0589/503A	Warmbad – Badplaas	0677/188	Vulcanus – Hosp
0589/543	Doornfontein	0677/259	Bergzicht
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0633/185	Bacchus	0724/790	Shangoni
0633/374	Klipsspruit	0734/773	Pelican Point
0633/429	Sterkrivier – Nedersetting	0734/897	Walvisbaai
0633/881	Potgietersrus – SKL	0735/011	Swakopmund
0635/076	Chuniespoort – POL	0737/527	Donkerhuk
0635/554	Malipsdrif – POL	0738/435	Tsawisis
0636/276	The Heights	0738/519	Abochaibis
0636/308	The Downs	0739/366	Neuheusis
0637/070	Harmony	0740/575	Voightland
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0639/504	Satara	0740/792	Hohenau
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0650/836	Solitaire	0741/587	Kleefforte
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0743/738	Spatzenfeld	0783/703	Dusterbrook
0744/419	Rosendal	0783/768	Otjiseva
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0745/145	Elsdale	0784/598	Neudam (Proefplaas)
0745/431	Humpata	0784/630	Neudam Agri. College
0762/372	Essexvale	0784/720	Sonneleiten
0762/532	Droëlei	0784/723	Otjonozonjati
0762/655	Matikulu	0784/826	Otjituezu Oos
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0763/675	De Gracht	0785/183	Otjikundua
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0764/385	Carlow	0785/297	Excelsior
0764/710	Omloop	0785/490	Okahua
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0768/011	Punda Maria	0812/567	Pafuri
0781/108	Dorstrivier		Beit Bridge
0781/227	Kubas		Maputo
0781/309	Ababbis Ost		Canigada
0781/522	Goas		Quissico
0781/815	Okongava Ost		Inhambane
0782/873	Erora Ost		Mabote
0783/534	Godeis		Vilanculos

**APPENDIX 2 : TEMPERATURE STATIONS SHOWING NUMBER USED IN FIG. 12,  
STATION NUMBER (S.A. WEATHER BUREAU) AND STATION NAME**

**Grassland Biome**

No.	Station no.	Station name	29.	57/048	Grahamstown–Vet
1.	79/811	Dohne–Agr	30.	59/572	East London–WK
2.	123/683	Queenstown–Mun	31.	96/045 A3	Graaff Reinet
3.	179/864	Mt Frere	32.	129/068	Cape Hermes
4.	205/385	Quthing	33.	182/794	Port Shepstone–Vrt
5.	233/044	Wepener–Tnk	34.	211/661	Umbogintwini
6.	239/482	Cedara	35.	240/649 A7	Pinetown–Mun
7.	268/631	Estcourt–Agr	36.	240/808	Louis Botha–WK
8.	303/833 A3	Eshowe–Mun	37.	241/072	Mount Edgecombe
9.	328/636	Virginia–Mun	38.	290/468	Kimberley–WK
10.	331/520	Loch Lomond	39.	323/102	Koopmansfontein–Agr
11.	366/743	Lindley–Mun	40.	339/357	River View
12.	370/765	Newcastle–Tnk	41.	360/597	Vaalharts–Agr
13.	437/134	Potchefstroom–Agr	42.	393/778	Kuruman
14.	438/550	Van der Bijl Park–Iscr	43.	410/709	Lavumisa
15.	444/126	Athole–Agr	44.	464/783	Tsabong
16.	472/279	Lichtenburg–Tnk	45.	483/053	Mpisi
17.	474/680	Carletonville	46.	511/523	Rustenburg–Agr
18.	475/456	Krundersorp–Mun	47.	511/855	Buffelspoort–Agr
19.	476/072	Johannesburg–Joubert Park	48.	513/284	Pretoria–Pur
20.	476/103	Johannesburg – City Deep	49.	519/017	Barberton–Agr
21.	476/398	Jan Smuts–WK	50.	546/630	Marico–Irr
22.	478/837	Bethal–Mun	51.	555/663 A8	D R de Wet–Bos
23.	480/184	Carolina–Tnk	52.	556/460	Pretoriuskop
24.	517/039	Belfast–Bos	53.	589/594	Toowoomba–Agr
25.	554/816	Lydenburg–Vis	54.	595/032	Fleur de Lys
			55.	596/179	Skukusa
			56.	634/011	Potgietersrus
			57.	639/504	Satara
			58.	680/167	Chester
			59.	719/370	Marnitz
			60.	740/154	Windhoek–WK
			61.	766/863	Gooldville–Hos
			62.	810/080	Messina
			63.	679/135	Belvedere
			64.	723/071	Lemana

**Savanna Biome**

No.	Station no.	Station name	60.	740/154	Windhoek–WK
26.	34/767	Uitenhage–Pur	61.	766/863	Gooldville–Hos
27.	35/179	Port Elizabeth–WK	62.	810/080	Messina
28.	54/805	Hillside Farm	63.	679/135	Belvedere
			64.	723/071	Lemana

**Nama-Karoo Biome**

No.	Station no.	Station name
65.	50/887	Willowmore—Mun
66.	74/296	Jansenville
67.	88/293	Sutherland
68.	98/190	Craddock—Tnk
69.	113/025	Fraserburg
70.	141/264	Victoria West—Aer
71.	145/059	Grootfontein—Agr
72.	170/009	De Aar—Agr
73.	175/371	Aliwal North
74.	193/561	Van Wyksvlei
75.	203/043	Smithfield—Mun
76.	225/679	Kareekloof
77.	229/556	Fauresmith
78.	258/157	Rietrivier—Agr
79.	259/390	Kalkfonteindam
80.	317/447	Upington—Agr
81.	419/184	Keetmanshoop—WK
82.	568/817	Mariental

**Succulent Karoo Biome**

No.	Station no.	Station name
83.	23/710	Robertson—Agr
84.	28/335	Oudtshoorn—Con
85.	43/516	Spes Bona
86.	106/850	Vredendal

87.	134/748	Calvinia—Tnk
88.	214/636	Okiep
89.	242/644	Port Nolloth
90.	274/034	Alexander Bay
91.	413/158	Diaz Point

**Desert Biome**

No.	Station no.	Station name
92.	649/064	Gobabeb
93.	734/773	Pelican Point

**Fynbos Biome**

No.	Station no.	Station name
94.	4/723	Tokai—Bos
95.	5/545	Somerset West—Dyn
96.	10/456	Riversdale
97.	12/251	Cape St Blaize
98.	20/719	Table Mountain—Hse
99.	20/866	Cape Town—CSIR
100.	21/656	Welgevallen—Agr
101.	21/793	Paarl—Agr
102.	28/748	George—WK
103.	43/566	Matroosberg
104.	39/781	Saldanha—Vlt

**Forest Biome**

No.	Station no.	Station name
105.	30/297	Diepwalle



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MEMOIRS VAN DIE BOTANIESE OPNAME VAN SUID-AFRIKA

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